National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service

Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

NL-339 (r. 88/04) c

Canada

UNIVERSITY OF ALBERTA

SOCIAL ORGANIZATION OF HAZEL GROUSE AND ECOLOGICAL FACTORS INFLUENCING IT

by

JON EUGENE SWENSON ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1991

National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-70055-6

Canada

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: JON EUGENE SWENSON

TITLE OF THESIS: SOCIAL ORGANIZATION OF HAZEL GROUSE AND ECOLOGICAL FACTORS INFLUENCING IT

DEGREE: DOCTOR OF PHILOSOPHY

YEAR GRANTED: FALL 1991

PERMISSION IS HEREBY GRANTED TO THE UNIVERSITY OF ALBERTA LIBRARY TO REPRODUCE SINGE COPIES OF THIS THESIS AND TO LEND OR SELL SUCH COPIES FOR PRIVATE, SCHOLARLY OR SCIENTIFIC RESEARCH PURPOSES ONLY.

THE AUTHOR RESERVES OTHER PUBLICATION RIGHTS, AND NEITHER THE THESIS NOR EXTENSIVE EXTRACTS FROM IT MAY BE PRINTED OR OTHERWISE REPRODUCED WITHOUT THE AUTHOR'S WRITTEN PERMISSION.

(SIGNED) Jon Swenson

PERMANENT ADDRESS:

6223 Shepherd Road East
Shepherd
Montana 59079 USA

DATE 18 June 1991

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SOCIAL ORGANIZATION OF HAZEL GROUSE AND ECOLOGICAL FACTORS INFLUENCING IT submittee by JON EUGENE SWENSON in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Supervisor

J. F. Bendell

External Examiner

Date June 18, 1991

ABSTRACT

The hazel grouse (Bonasa bonasia) is a small (<400 g) grouse that inhabits Palearctic boreal and montane forests. I studied the social organization of hazel grouse and ecological factors influencing it in Sweden (yearlong) and Siberia (winter). The two most important factors I documented were the abundance and dispersion of food and the risk of predation. During the breeding season, females have high nutritional requirements. They were territorial, and defense of limited nutritious food appeared to be more important than nest guarding or nest dispersion in promoting territoriality. The social unit was a pair, but females were more often (>37%) with another male than males were with another female (>3%). Monogamous mating appeared to be promoted by female territoriality, the apparent female need of vigilance, male and female territories of the same size, a male-biased sex ratio, and synchronous breeding. The pair bond was weaker in secure habitats, where the potential for polandry was higher. During the nonbreeding period in spruce forests, males and females exhibited intrasexual territoriality, except in summer. The social unit was the pair, although it was not exclusive. The pair appeared to be a compromise between defense of winter food and need of a partner for vigilance while foraging in open sites. In open riparian forests where food was abundant, hazel grouse formed flocks. Flock size varied inversely with cover, consistent with the hypothesis that flocking was a predator protection response. Small species require nutritious food. Alder (Alnus glutinosa & A. incana), highly preferred as winter food in Fennoscandia, is very nutritious, especially the catkins, but it is uncommon and patchily distributed. Hazel grouse abundance and distribution varied with that of alder at four levels of scale. Survival was spatially heterogenious; 95% of the variation was explained by variation in forest structure. Two-layered forests were more secure than one-layered forests. Heterogeniety in winter food and survival appeared to contribute to population regulation. Adults established territories two to four weeks before juveniles in autumn and many birds, probably mostly juveniles, established in dangerous habitats where they were killed in early winter. Insights from this study were used to form hypotheses about important factors in the evolution of mating systems, territoriality, winter flocking, and population regulation by social behavior in grouse.

ACKNOWLEDGMENTS

During this research, I received support from the Fulbright Program (research fellowship), the Department of Zoology, University of Alberta (research assistantships and a travel grant), the McAfee Estate, Stiftelsen Olle Engkvist, Byggmästare, the Natural Sciences and Engineering Council of Canada (to Dr. D. A. Boag), the American-Scandinavian Foundation, the Grimsö Wildlife Research Station, the Swedish Environmental Protection Agency, the Swedish Sportsman's Association, the Department of Biology, University of Oslo (to Johan Danielsen), the Academy of Sciences of the USSR, and the Nordic Collegium for Wildlife Research. I thank all of these foundation and agencies for their support.

Many people helped me during this project. My academic committee provided valuable guidance at the beginning of this study and many helpful comments during it: D. A. Boag, S. A. Boutin, S. J. Hannon, and G. H. La Roi. Those that have invested a significant amount of time in the field are Sasha Andreev, Johan Danielsen, Sergei Drovetskii, Bill Faber, Per Grängstedt, Carin Hansson, Ulrika Hjelm, Petter Kjellander, Björn Olsson, Volodya Pravosudov, Steve Redpath, Andrew Schoepf, Kent Sköld, and Trevor Wiens. I truly appreciate the help and I enjoyed the company of all of you. We made a fine team. Johan Danielsen, my first student, taught me that I could take time out to enjoy myself in the field and still get the job done. Wolfgang Scherzinger provided recordings of hazel grouse vocalizations and Martin Forster provided the "Wursperl" whistle, with directions, so I could imitate the female aggressive call. All of the people at Grimsö provided friendship and an unbelievably rich and productive research environment. I have enjoyed it so much that I look forward to continued work with you. Especially, I would like to thank Per Angelstam for inviting me to Grimsö, P. A. Lemnell for allowing it, and Per, Henrik Andrén and Erik Lindström for stimulating discussions, pointing out alternative hypotheses, and for help with the computer and methods of analysis.

This thesis was improved greatly by the comments of David Boag, Jim Bendell, Henrik Andrén, Sasha Andreev, Per Angelstam, Susan Hannon, Ingemar Jönsson, Erik Lindström, Steve Redpath, Jørund Rolstad, Jim Schieck, Bob Small and Tomas Willebrand.

David Boag, my supervisor, deserves a special thanks. You were enthusiastic about this project from the start to the finish, and you believed in me and the project even when I had my doubts. You also gave me a perfect blend of guidance and freedom. I am amazed at how well you served as my supervisor at such a distance. Per Angelstam was my advisor at Grimsö. He did this admirably, also giving me freedom, but always there when I needed advice or gentle steering. I also wish to thank my former advisor, Bob Eng, for his encouragement when I decided to pursue a PhD and for helping me contact David Boag, and Sasha Andreev, for introducting me to the cold larch forests of northeastern Siberia and the warm people who live there.

My parents deserve thanks for supporting me (us) in this effort. As in all of

my other endeavors, you did not ask me if I had thought it through or if I was crazy to leave a permanent job that I enjoyed to try to study a bird I had never seen in a place I had never been thousands of miles from a university I had never visited. You knew that I knew it was right. I would never have accomplished what I have without support like that. I would also like to thank my parents-in-law for all their help and support.

I cannot imagine how I could have completed this project without Hanne, my wife and best friend. You were so supportive of me, as you always have been (and still are!). You were happy to return to your native Scandinavia, but perhaps only I can appreciate how hard you have worked to move a household from Montana to Alberta to Montana to Norway and to three places in Sweden and to work nights to help support us. It still amazes me how quickly and effectively you could turn those houses into warm and cheerful homes, especially when virtually everything we had was borrowed. It has been great fun though, hasn't it? Our children, Frank Olav and Eva Kristine, still do not really understand that Pappa can still be going to school when he has gray hair. I want to thank you for the joy you have given me, the fun we had in the "jerpeskogen", roasting hot dogs and relocating hazel grouse, and the help in catching grouse. I have wondered how you could be so excited about hazel grouse when they took so much of my time from you, but the tears you cried when I came home with parts of a dead radio-marked grouse were real.

TABLE OF CONTENTS

Chapter Page

I. THESIS INTRODUCTION 1

THE QUESTION. 1

THE SPECIES 2

LITERATURE CITED 3

II. SOCIAL ORGANIZATION OF HAZEL GROUSE DURING THE BREEDING PERIOD: ARE THEY MONOGAMOUS? 6

INTRODUCTION 6

STUDY AREA AND METHOD. 6

RESULTS 9

Social organization 9

Mating tactics. 12

Comparison of spring and autumn territoriality. 15

DISCUSSION. 15

Social organization 15

Mating system. 21

Monogamy in hazel grouse 22

LITERATURE CITED 23

III. FACTORS PROMOTING FEMALE TERRITORIALITY AND MONOGAMY IN HAZEL GROUSE. 27

INTRODUCTION 27

STUDY AREA AND METHODS 29

RESULTS 30

Factors promoting female territoriality and aggression. 31

The food shortage hypothesis 31

The nest dispersion hypothesis. 34

The nest guarding hypothesis 38

Factors promoting monogamous mating. 38

The male sentry hypothesis 38

The mate guarding hypothesis 42

The demography hypothesis 42

DISCUSSION. 42

Factors promoting female territoriality 42

Factors promoting monogamous mating. 45

The mating system in hazel grouse 46

The mating systems of the subfamily Tetraoninae 48

Was the ancestral grouse monogamous?. 52

LITERATURE CITED 53

IV. SOCIAL ORGANIZATION OF HAZEL GROUSE DURING THE NONBREEDING PERIOD AND ITS CONSEQUENCES FOR POPULATION REGULATION 61

INTRODUCTION 61

STUDY AREA AND METHODS. 62

RESULTS. 63

Timing of autumn territoriality 63

Size and spatial arraingement of territories 65

Indications of territorial aggression 70

Replacements in territories following their vacancy. 77

Variation in territory quality 80

Survival 80

Reproductive success 80

Winter food resources 80

Seasonal changes in population size 82

DISCUSSION 82

Social organization 82

What is being defended? 87

Autumn territoriality and population regulation 88

Population regulation and population stability 89

Comparison with other species of grouse 91

LITERATURE CITED 92

V. RELATIONSHIPS BETWEEN MALE AND FEMALE HAZEL GROUSE DURING THE NONBREEDING SEASON 100

INTRODUCTION 100

STUDY AREA AND METHODS 101

RESULTS 102

Territorial overlap and spatial relationships between males and females 102

Winter foraging behavior when alone and together 104

DISCUSSION 108

LITERATURE CITED 110

VI. FACTORS SHAPING WINTER SOCIAL ORGANIZATION IN HAZEL GROUSE: A COMPARATIVE STUDY IN THE EASTERN AND WESTERN PALEARCTIC. 113

INTRODUCTION. 113

STUDY AREAS. 114

METHODS. 115

RESULTS 116

Size and composition of winter groups 116

Behavior of birds in groups 118

Cover at foraging sites. 120

Distribution and abundance of winter food 122

DISCUSSION. 126

LITERATURE CITED 130

VII. THE IMPORTANCE OF ALDER TO HAZEL GROUSE IN FENNOSCANDIAN BOREAL FOREST: EVIDENCE FROM FOUR LEVELS OF SCALE 135

INTRODUCTION 135

STUDY AREA 136

METHODS 136

RESULTS 138

Food selection by hazel grouse 138

Dispersion pattern and habitat of black alder. 144

Distribution of alders and hazel grouse: level of territory (ca. 20 ha). 144

Abundance of alders and hazel grouse: level of local patch (5 km^2) 148

Distribution of alders and hazel grouse: level of landscape (140 km^2) 148

Abundance of alder and hazel grouse: level of biogeographic region (337,000 km^2) 148

DISCUSSION. 148

Selection of winter food. 148

Does winter food limit numbers and/or distribution? 153

The population consequences of being an alder specialist 155

LITERATURE CITED 155

VIII. SMALL-SCALE SPATIAL HETEROGENIETY IN SURVIVAL RATES OF TERRITORIAL HAZEL GROUSE 159

INTRODUCTION 159

STUDY AREA 159

METHODS 160

RESULTS 161

Effects of the transmitters 162

The predators 162

Seasonal and sexual variation in survival rates 162

Spatial pattern of survival 162

Occurrence of kill sites in relation to forest structure 167

Survival rates and forest characteristics of generalized territories 167

DISCUSSION 171

Spatial heterogeniety of survival rates 171

Hazel grouse survival and habitat selection by the predators 172

Effect of transmitters on survival 173

LITERATURE CITED 173

IX. THESIS DISCUSSION 177

SOCIAL ORGANIZATION IN HAZEL GROUSE 177

Territoriality 177

Relationships between individuals 178

Mating system 178

IMPORTANT ECOLOGICAL CONSTRAINTS 179

Body size 179

Abundance and dispersion of food 179

Predation 180

ECOLOGICAL RAMIFICATIONS 181

Population regulation 181

Spatial dispersion of habitats. 181

Evolution of grouse mating systems 182

LITERATURE CITED 182

LIST OF TABLES

Table Page

II-1 Number of birds of the opposite sex with hazel grouse during the prelaying and relaying receptive periods. 13

II-2 Sex ratio of hazel grouse on the study area on 1 May 14

III-1 Clutch sizes of hazel grouse on the Grimsö Wildlife Research Area, 1988-1990. 37

III-2 Survival rates of radio-marked female and male hazel grouse during the late winter and spring, 1988-1990 39

III-3 Degree of female territoriality among grouse during the prelaying period, measured as overlap of neighboring territories, in relation to the body mass of females and type of habitat. 50

IV-1 Size and mean overlap of territories of radio-marked male and female hazel grouse on the study area during summer, autumn, and winter 69

IV-2 Degree of overlap of seasonal territories of individual hazel grouse on the study area 74

IV-3 Responses of territorial female hazel grouse to an imitation of the aggressive hen call in autumn 77

IV-4 Censuses of territorial male hazel grouse in autumn and spring on the study area (195 ha of forest) and response time to the imitation of the territorial song in autumn 78

IV-5 Number of preferred alders within territories of male and female hazel grouse on the study area in summer, autumn, and winter. 81

V-1 Effects of sex and number of birds on foraging rate (seconds used to take 20 bites) of hazel grouse foraging in black alder in winter. 105

V-2 Characteristics of sites used by arboreally foraging hazel grouse when alone or with another bird in winter 106

VI-1 Sizes of winter groups of hazel grouse in Siberia and Sweden in different forest types. 117

VI-2 Cover and forest density at winter foraging sites of hazel grouse in riparian forest (Yana Valley, Siberia) and spruce forest (Grimsö, Sweden) in relation to group size 121

VI-3 Number of trees, by category, within 10 m of sites of hazel grouse foraging in the Yana Valley and at Grimsö in relation to the surrounding forest 123

VI-4 Use of deciduous trees for winter foraging by hazel grouse in the Yana Valley, Siberia, and Grimsö, Sweden 124

VI-5 Abundance and dispersion of hazel grouse winter food trees in three areas (two in Siberia and one in Sweden) 125

VI-6 Most common group size in winter among hazel grouse in relation to winter habitat in 27 localities throughout the species' range (based on 20 reports in the literature and this study). 129

VII-1 Use of deciduous trees by foraging hazel grouse relative to their occurrence on the study area over three winters 139

VII-2 Number and biomass of staminate catkins and buds within the crowns of three black alder trees from Halden, Norway, winter 1988-89. 142

VII-3 Location of foraging hazel grouse in tree canopies in winter, Grimsö Wildlife Research Area 143

VII-4 Selected habitat variables relative to the occurrence of alder trees (>3 m tall) on 566 plots on the study area, Grimsö Wildlife Research Area 146

VII-5 Distribution of hazel grouse relative to the distribution of alder on 25-ha blocks within the Grimsö Wildlife Research Area (data from 1977-1987). 150

VIII-1 Seasonal survival rates of radio-marked male and female hazel grouse on a forest reserve (C.I. = confidence interval) 163

VIII-2 Annual survival rates of territorial hazel grouse in nine generalized territories within the study area (C.I.= confidence interval). 164

VIII-3 Seasonal survival of hazel grouse in the northern part (generalized territories A-E) and southern part (F-I) of the study area. 166

VIII-4 Distribution of sites where hazel grouse were found dead in relation to forest structural categories on the forest reserve 168

VIII-5 Distribution of 24 hazel grouse kills and 24 random points in relation to distance (in m) from various edges 169

LIST OF FIGURES

Figure Page

II-1 Overlap of territories of radio-marked male (lines) and female (shaded) hazel grouse during the breeding season 10

II-2 Timing of leaving territories by radio-marked male hazel grouse in the spring and timing of replacement or not of radio-marked territorial female hazel grouse 11

II-3 Monthly indices of spontaneous territorial advertisement on the study area (instances per 10 field days) and of responses to an imitation of the territorial song (instances per 5 field days) in southern Finland (from Pynnönen 1954:69). 16

II-4 Monthly indices of border disputes by radio-marked male and female hazel grouse on the study area. 17

II-5 Monthly indices of activity of radio-marked male and female hazel grouse on the study area. 18

II-6 Monthly rates of movement of radio-marked male and female hazel grouse on the study area. 19

III-1 Body mass of male and female hazel grouse in relative to the onset of laying in late spring 32

III-2 Relationship between size of female hazel grouse territories and the density of spring food. 33

III-3 Relationship between hazel grouse egg mass and clutch size on and near the study area in southcentral Sweden 35

III-4 Relationship between hazel grouse egg mass and clutch size on Hokkaido Island, Japan (from Haga & Takamata 1986). 36

III-5 Variations in intrapair distance (simultaneously obtained locations between the male and female of a pair of hazel grouse, all pairs combined) during the prebreeding and breeding seasons on the intensive study area. 40

III-6 Relationship between interpair distances of hazel grouse pairs and the security of their territories, as determined by annual survival of radio-marked hazel grouse during the prelaying fertile period and renesting period 41

III-7 The relationship between spontaneous advertisement of male hazel grouse between 1 April and 15 May and the security of their territories, as determined by annual survival of radio-marked hazel grouse. 43

III-8 Relationship between the body mass of female grouse and their social behavior during the premating period in open and forested habitats (based on reviews in Hjorth 1970, Johnsgard 1983, Klaus et al. 1989, 1990). 49

IV-1 Monthly indices of spontaneous territorial advertisement on the study area (instances per 10 field days) and of responses to an imitation of the territorial song (instances per 5 field days) in southern Finland (from Pynnönen 1954:69) during the nonbreeding season. 64

IV-2 Monthly indices of border disputes by radio-marked male and female hazel grouse on the study area during the nonbreeding season. 66

IV-3 Monthly indices of activity of radio-marked male and female hazel grouse on the study area during the nonbreeding season. 67

IV-4 Monthly rates of movement of radio-marked male and female hazel grouse on the study area during the nonbreeding season . . . 68

IV-5 Map of territorial boundaries of male and female hazel grouse during summer on the study area. 71

IV-6 Map of territorial boundaries of male and female hazel grouse during autumn on the study area. 72

IV-7 Map of territorial boundaries of male and female hazel grouse during winter on the study area 73

IV-8 Relationship between degree of territory overlap with nearest neighbor and winter territory size for males on the study area. 75

IV-9 Rates of known territory acquisiton following the death or emigration of a radio-marked territorial hazel grouse throughout the year on the study area. 79

IV-10 Relationship between decline in hazel grouse counts from summer to autumn and summer counts, based on line transects, in the Bialowieza Forest, Belorussia, during 1948-51. 83

IV-11 Means and variation (standard deviation) of hazel grouse counts based on line transects during three seasons of each year, 1948-51, in the Bialowieza Forest, Belorussia, during 1948-51. 84

IV-12 Summary of timing of important events in the social organization of hazel grouse during August through March. 85

V-1 Overlap of territories of radio-marked male (lines) and female (shaded) hazel grouse during autumn and winter 103

V-2 Use of alder trees ≥10 m tall by hazel grouse foraging alone and together in relation to distance from continuous spruce forest. 107

VI-1 Percentage of juvenile hazel grouse in monthly samples of hazel grouse collected in Yana Valley, Siberia during the 1988-89 winter. 119

VII-1 Occurrence of alders used by foraging hazel grouse and all alders >10 m tall in relation to distance from spruce forest on the study area in southcentral Sweden. 141

VII-2 Distribution of alder on the Grimsö Wildlife Research Area 145

VII-3 Relationship between winter territory size and density of preferred alders on the study area 148

VII-4 Counts of territorial male hazel grouse on the western and eastern halves of the forest reserve, Grimsö Wildlife Research Area 149

VII-5 Relationship between mean relative hazel grouse density from 1964 to 1977 and proportion of forests dominated by alder in Finland. 151

VII-6 Relationship between mean relative hazel grouse density from 1964 to 1977 and proportion of forests dominated by birch in Finland. 152

VIII-1 Map of the study area, indicating annual survival rates of territorial hazel grouse within the nine generalized territories. 165

VIII-2 Relationship between the annual survival rate of territorial hazel grouse and proportion of category 2 forest (both arcsine transformed) in the generalized territories on the study area. 170

I. THESIS INTRODUCTION

THE QUESTION

All species are faced with variation in environmental conditions, including variation that exceeds the limits of survival for individuals of the species. A hypothetical n-dimensional hypervolume enclosing all the environmental limits to survival describes the species' niche, in the Hutchinsonian sense of the term (Hutchinson 1958, 1968). Within this niche space, individuals of the species can respond to variations in environmental variables through morphological, physiological, and/or behavioral adaptations. In the 1960's, it was realized that the social organization, including mating system, of a species also could be viewed as an adaptation to ecological constraints, and not necessarily products of the species' phylogenetic heritage (Vehrencamp & Bradbury 1984). Orians (1961) stressed differences in the spatial and temporal dispersion of food as the major factor shaping different social and mating systems in blackbirds (Icteridae), and Crook (1964) concluded that this variable and differences in defense against predators were the factors responsible for the variation in social organization and mating systems in weaverbirds (Ploceidae). Verner (1964), Verner & Willson (1966) and Orians (1969) stressed the importance of habitat productivity in determining the potential for polygyny among passerines (Passeriformes). Brown (1964) recognized that the spatial and temporal variation in food abundance had to be viewed within the context of the individual's ability to defend it. He introduced the idea of economics to social organization, comparing the costs of defending a territory with the benefits gained.

Davies & Krebs (1978) define social organization by referring to the following characteristics of a species: breeding and feeding group size (e.g. solitary, flocking); spatial organization (e.g. territorial, overlapping ranges); and mating system (e.g. monogamy, polygyny). It is now widely accepted that ecological variables impose limits on the range of types of social organization that are adaptive, apparently determined by the relative costs and benefits of different forms of social organization to individuals. This implies that many aspects of an animal's social organization can be predicted on the basis of an understanding of a limited set of environmental variables (Emlen & Oring 1977, Gosling & Petrie 1981, Pulliam & Millikan 1982). The objectives of my study were to document the social organization of hazel grouse (Bonasa bonasia), to identify the ecological constraints that are important in shaping and maintaining it, and to examine its ramifications in terms of the potential for population regulation through intrinsic means and other aspects of the species' ecology. My study was conducted over the annual cycle to determine if ecological constraints and social organization varied through the year.

The range and gradations of social organization and mating systems among the 17 grouse species (subfamily Tetraoninae) are among the greatest within an avian subfamily (Wiley 1974). They also form a closely related group (Short 1967). Thus, it is a convenient group for comparative studies of social organization and mating systems. I chose to study the hazel grouse for several reasons. First, it appeared to be an "exception to the rule" in many respects, which could provide insights into the important ecological factors influencing social organization in the other forest grouse and perhaps all the grouse. For example, the hazel grouse, and the little known black-breasted hazel grouse (B. sewerzowi) of China, are the only forest grouse thought to be monogamous and the former is the only forest grouse believed to defend a territory throughout the year (Bergmann et al. 1982). Second, a social or mating system is a result of the behavior of individuals; among hazel grouse there was evidence of behavioral variation among individuals. Some apparently overwinter in pairs and others alone (Pynnönen 1954). Moreover, in the western Palearctic hazel grouse overwinter singly or in pairs but in flocks in the eastern Palearctic (Bergmann et al. 1982, Potapov 1985). Unmated males in spring are commonly observed (Pynnönen 1954, Tomek 1965, Hjort 1970, Wiesner et al. 1977), and Lindén & Wikman's (1983) study suggested that survival varied by habitat type within a local area. The third reason was the challenge of studying a relatively poorly known species. Although much has been written about hazel grouse ecology, the only study of social organization was conducted by a Finnish school teacher in his free time (Pynnönen 1954); to date, no studies have been published based on data from individually marked birds. This paucity of background data created a number of problems, including the practicality of capturing birds for marking and an inability to perform experiments because not enough data were available to design experiments. A fourth reason for choosing the hazel grouse was the opportunity to contribute knowledge to help conserve a vulnerable species. Many hazel grouse populations are extinct and numbers are declining throughout much of its range (Swenson & Danielsen 1991).

THE SPECIES

The hazel grouse is a small, quiet, and shy grouse that lives in dense vegetation, making it difficult to study (Bergmann et al. 1982). Hazel grouse are sexually monomorphic in size, weighing 375-400 g; only two grouse species are smaller, the Asian black-breasted hazel grouse, ca. 250-300 g, and the North American white-tailed ptarmigan (Lagopus leucurus), 300-350 g (Johnsgard 1983). The hazel grouse has an extensive range throughout the Palearctic boreal forest from the western coast of Norway to northeastern Siberia, and extending southwards into central France, Yugoslavia, North Korea, and the Japanese island of Hokkaido (Bergmann et al. 1982).

The hazel grouse has the narrowest niche of European grouse (Seiskari 1962). It requires dense coniferous cover, primarily Norway spruce (Picea abies) and/or white fir (Abies alba) with a high degree of canopy closure, a dense coniferous understory, and a supply of deciduous trees for catkins and buds as winter food, which in Fennoscandia are alder (Alnus glutinosa and A. incana) and birch (Betula pubescens and B. pendula). Because of this double requirement of heavy coniferous cover and deciduous trees, hazel grouse in Europe inhabit primarily spruce forests with an old-growth structure, where wind throw, snow damage, or small-scale forestry have opened small gaps that are colonized by birch or alder and young spruces, or successional stages after burning or clearcutting that provide sufficient cover and deciduous trees (review in Bergmann et al. 1982).

Hazel grouse territories purportedly are defended throughout the year, but territorial behavior is most evident in the autumn, when juveniles establish territories, and spring, during the breeding season (Pynnönen 1954, Ivanter 1962, Zbinden 1979). The hazel grouse is thought to be monogamous; a pair bond purportedly exists almost all year, but the male does not participate in rearing the brood (Bergmann et al. 1982). Further information on the life history of hazel grouse is summarized well in Bergmann et al. (1982).

LITERATURE CITED

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Crook, J. H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour Suppl. 10:1-178.

Davies, N. B. & J. R. Krebs. 1978. Introduction: ecology, natural selection and social behaviour. Pp. 1-18 in J. R. Krebs & N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford.

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Gosling, L. M. & M. Petrie. 1981. The economics of social organization. Pp. 315-382 in C. R. Townsend & P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Hjorth, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7:183-596.

Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:415-427.

Hutchinson, G. E. 1968. When are species necessary? Pp. 177-186 in R. C. Lewontin, ed. Population biology and evolution. Syracuse Univ. Press, Syracuse, New York.

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In

Russian)

Johnsgard, P. A. 1983. The grouse of the world. Univ. Nebraska Press, Lincoln.

Lindén, H. & M. Wikman. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. J. Anim. Ecol. 52:953-968.

Orians, G. H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31:285-312.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 100:589-603.

Potapov, R. L. 1985. Fauna SSSR, ptitsy, otryad kyroobraznye (Galliformes), semeistvo teterevinye (Tetraonidae). Nauka, Leningrad. (In Russian)

Pulliam, H. R. & G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biol. 6:169-197.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Short, L. L., Jr. 1967. A review of the genera of grouse (Aves, Tetraoninae). Am. Mus. Novitates No. 2289.

Sieskari, P. 1962. On the winter ecology of the capercaillie, Tetrao urogallus, and the black grouse, Lyrurus tetrix, in Finland. Pap. Game Res. 22:1-120.

Swenson, J. E. & J. Danielsen. 1991. The status and conservation of the hazel grouse in Europe. Ornis Scand. 22:in press.

Tomek, W. 1965. Hazel hen in Ciezkowice Highlands, southern Poland. Przeglad Zool. 9:395-404. (In Polish, English summ.)

Vehrencamp, S. L. & J. W. Bradbury. 1984. Mating systems and ecology. Pp. 251-278 in J. R. Krebs & N. B. Davies, eds. Behavioural ecology, an evolutionary approach, 2nd ed. Blackwell Sci. Publ., Oxford.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18:252-261.

Verner, J. & M. F. Willson. 1966. The influence of habitats on mating systems of North American passerines. Ecology 47:143-147.

Wiesner, J., H.-H. Bergmann, S. Klaus & F. Müller. 1977. Siedlungsdichte und Habitatstruktur des Haselhuhns (Bonasa bonasia) im Waldgebiet von Bialowieza (Polen). J. Ornithol. 118:1-20.

Wiley, R. H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49:201-227.

Zbinden, N. 1979. Zur Ökologie des Haselhuhns Bonasa bonasia in den Buchenwäldern des Chasseral, Faltenjura. Ornithol. Beob. 76:169-214.

II. SOCIAL ORGANIZATION OF HAZEL GROUSE DURING THE BREEDING PERIOD: ARE THEY MONOGAMOUS?

INTRODUCTION

Grouse have received considerable attention in the study of mating systems because the species in the subfamily (Tetraoninae) are closely related, yet exhibit a wide spectrum of mating systems, including monogamy (Wiley 1974). The species reported to be monogamous include the willow, rock, and white-tailed ptarmigan (Lagopus lagopus, L. mutus, and L. leucurus), all tundra species, the hazel grouse (Bonasa bonasia), occupying Palearctic boreal and montane forests (Hjorth 1970), and the black-breasted hazel grouse (B. sewerzowi), occupying montane forests in southeastern China (Wang et al. 1987). Even among these species, the degree of monogamy appears to be variable. For example, the mating system of rock ptarmigan varies from monogamous to polygynous or even promiscuous (Vinokurov 1983, Unander & Steen 1985, Brodsky 1988, Gardarsson 1988).

There is wide agreement that the hazel grouse is monogamous (Donaurov 1947, Pynnönen 1954, Ivanter 1962, Dement'ev et al. 1967, Hjorth 1970, Glutz von Blotzheim et al. 1973, Scherzinger 1981, Bergmann et al. 1982). Apparently only Potapov (1985) has questioned whether the hazel grouse is always monogamous. In comparative studies of grouse mating systems, the hazel grouse always has been considered as monogamous (Vos 1979, Hjorth 1970, Wiley 1974, Wittenberger 1978). The monogamy referred to in the references about hazel grouse was an inferred monogamous social organization, because one male and one female are often seen together (although none of these studies were based on marked birds), but in the studies of grouse mating systems, hazel grouse were assumed to have a monogamous mating system. Wickler & Seibt (1983) have stressed the importance of distinguishing between monogamy as a social unit and as a mating tactic.

The objectives of this study were to document the social organization of hazel grouse during the breeding season and to determine if they are monogamous. Monogamy was examined both as a social unit during the breeding season, indicating the association of two individuals of opposite sex, and as an individual's mating tactic, indicating an exclusivity in reproduction (Wickler & Seibt 1983). Here I present descriptive data; hypotheses about the factors promoting reproductive monogamy are examined in Chapter III.

STUDY AREA AND METHODS

The study area (285 ha, 195 ha of forest) was within a forest reserve on the Grismö Wildlife Research Area in southcentral Sweden (59-60° N and 15-16° E). It is described in detail in Chapter VII.

The study encompassed three breeding seasons, 1988 through 1990, and was based on the use of radiotelemetry. Hazel grouse were captured in spring and autumn by luring or chasing them into nylon fishing nets. They received ca. 16-g necklace-type transmitters (Kenward 1987) that weighed ca. 4.5% of the birds' weight. Age category (yearling or adult) was determined by the coloration of the innermost primary (Stenman & Helminen 1974).

The breeding period was defined as April and May, determined *a priori* from behavioral data in an area of similar latitude (Pynnönen 1954). Territory locations and sizes were determined during each season for birds with 25 or more relocations using the method of Harvey & Barbour (1965). The majority of relocations were based on bearings, three if birds were >150 m away, and two if less. About 75% of the relocations were ≤20 m of the actual location (Chapter IV). Territory size was measured from a 1:15,000 map with a Kempten planimeter. Territory overlap was expressed as the mean percent overlap recorded for each territory and its neighbor. Neighbors were radio-marked birds with no known territories between them. Pairs were defined as a territorial male and female with territories that overlapped each other by more than 50% and that were with each other more than with others of the opposite sex during the breeding period. The term pair did not imply exclusive mating.

Pairs were considered to share the same space if 100% overlap was included in the 95% confidence interval of territory overlap of pairs. Also, a pair was considered to be a social unit if the male and female were located together (≤20 m apart) more often than by chance. This was determined by comparing the frequency that two randomly-chosen points within an average-sized territory were within 20 m, based on 200 replications.

The breeding season contained two periods when copulation could result in fertile eggs; the prelaying period and the renesting period. On average, incubation began on the study area on 17 May in 1988 (N=3), 14 May in 1989 (N=2), and 6 May in 1990 (N=4). Incubation began at all nests of radio-marked females within a five-day period each year (Chapter III). The laying interval between eggs for hazel grouse is about 1.3 days (Pynnönen 1954, Semenov-Tyan-Shanskii 1959), and the mean clutch size on the area was 7.6 eggs (Chapter III). The duration of fertility following copulation is not known for hazel grouse, but it averages 8 days in willow ptarmigan (Parker 1981) and 24 days in capercaillie (*Tetrao urogallus*) (Parker et al. 1989). Hazel grouse more closely resemble willow ptarmigan in size and mating system and have hybridized with them, but this has not been recorded with capercaillie (Johnsgard 1983). Also, Haga & Takamata (1986) observed a captive pair of hazel grouse copulate seven days before laying began and two days after the first egg was laid. Therefore, an eight-day fertile period prior to laying was assumed. Based on this, the prelaying receptive period began on 29 April in 1988, 26 April in 1989 and on 18 April in 1990. The renesting period began when a nest was destroyed and lasted until 15 June, the latest date incubation began at a renest by a radio-marked female during the study. In 1990, I removed the clutches of all four radio-marked females at the beginning of incubation and in 1989 I removed one late in incubation to obtain more data from the relaying period.

During the breeding season, radio-marked birds were relocated 5-15 times a week. During each receptive period, males and females that were not relocated with another radio-marked bird were approached as often as possible (50-75% of the instances) to determine if they were with an unmarked bird. No copulations were observed during this study, but it was assumed that all observations of a male and female together during the receptive periods could have resulted in copulation(s) and that a bird observed with more than one bird of the opposite sex during a given receptive period may have mated polygamously. This was a reasonable assumption because, in willow ptarmigan, which have a stronger pair bond than hazel grouse (see below), paired females accept copulations with intruder males during their receptive periods (Martin & Hannon 1988), and males can mate polygynously (Hannon 1983). Female rock ptarmigan also can mate with more than one male and males with more than one female (Vinokurov 1983, Brodsky 1988, Gardarsson 1988). Also, the occurrence of extra-pair copulations by females in monogamous and polygynous bird species appears to be more common than had been thought previously (Oring 1982, Björklund & Westman 1983, Alatalo et al. 1984, Gowaty & Karlin 1984, McKinney et al. 1984, Gowaty 1985), and no study has shown that engaging in extrapair copulations is disadvantageous to females (Björklund & Westman 1986).

I recorded all spontaneous advertisement heard in the field. Total rate of advertising was the number of bouts heard per field day. A border dispute was defined as an instance of two or more radio-marked birds of the same sex located within 60 m of each other at a territorial boundary. Unmarked birds also were included in this rate when they were heard exchanging territorial advertisement with a radio-marked bird near its boundary. An index of activity was based on the percentage of the relocations during a month that birds were recorded as being active. Activity of the birds was based on changes in signal strength during triangulation. Net movement in one day was defined arbitrarily as the distance between locations of a hazel grouse on consecutive days. All birds of each sex were combined to determine these rates because I was documenting patterns and performing no statistical tests. These indices were used to determine when the female was more active and mobile than the male, to learn when the female may have started using more time for foraging and may have been more vulnerable to predation.

To determine if females reacted aggressively towards intruders, their reaction to the hen call (Hennenruf, a female aggressive call, Scherzinger 1981) was tested in spring. A Wusperl whistle (Bergmann et al. 1982:34) was used to imitate the hen call. After locating a radio-marked female, I hid 50-150 m away. I then whistled once per minute for 20 minutes, checking signal strength every 5 minutes. Afterwards, I located the female to determine distance moved, and if not with a radio-marked male, I determined if a male was present. I used a mounted female to determine if the female would attack it only in 1989. A female was considered to respond positively (aggressively) if it approached or gave a territorial advertisement during the trial period. Other indications of territoriality for both sexes were little or no territorial overlap and a negative relationship between territory area and population density (Hixon 1987).

Sex ratio on 1 May was determined from intensive searches of portions of the study area where most of the territorial hazel grouse were radio-marked. The size of the area surveyed for sex ratio varied somewhat between years, depending on the locations of marked birds but included most of the study area each year. Each year, 60-100% of the males and 33-100% of the females were marked. Population density was determined for the entire study area each spring and was expressed as the number of males responding to an imitation of the territorial song per 100 ha (Swenson 1991).

Tests using 2x2 contingency tables were corrected for continuity with Yate's correction. Throughout the paper I have presented means with the standard error of the mean.

RESULTS

Social organization

During the breeding season, hazel grouse were territorial and in pairs, with each sex excluding members of the same sex from their territories. Male territories averaged 17.0±2.3 ha (N=15) in size and female territories 14.4±2.0 ha (N=7). These were not significantly different (t=0.72, df=21, two-tailed P=0.48). Territories of unpaired males averaged more than twice as large (32.2±2.8 ha, N=2) as those of paired males (14.6±1.9 ha, N=13, t=3.51, df=14, two-tailed P=0.004). Both unpaired males were adults that had lost their females to predators in early April. Territory size was negatively correlated with spring population density for both males (Spearman rank correlation, r_s= -0.482, df=13, P=0.04, one-tailed test) and females (r_s= -0.777, df=5, P=0.03). Both males and females appeared to maintain exclusive territories. Mean overlap between two neighboring birds of the same sex was 2.8±2.5% for males (N=13 pairs of neighbors). In one instance, described below, there was considerable overlap between the territories of two males (21% and 43%, mean of 32% shared). Excluding this case, mean overlap for males was 0.4±0.4% (N=12). No overlap was recorded between four pairs of neighboring females (Fig. II-1) and none of the 18 unmarked females observed on the study area during the spring were on the territory of a marked female.

Female territorial behavior was tested by imitating the female aggressive call within 100 m of 7 prelaying females. All of these females reacted positively, by approaching (six birds) and/or advertising (four or five birds; one advertisement may have been from the male). The advertisements were one song, two or three flutter jumps, and one female aggressive call.

The mean territorial overlap of males and females that were pairs (together with each other more than with any others) was 81±5% (N=6, Fig. II-1). Total overlap was included within the 95% confidence interval (52-110%). Pairs were together (≤20 m apart) 37±5% of the time during the prelaying period, significantly more than expected if the two birds were randomly distributed on the territory (expected=0%, Wilcoxon signed rank test, N=8, two-tailed P=0.012).

Males and females showed different temporal patterns when they changed territories (Fig. II-2). Four females killed during November through February were replaced by a new female before the next breeding season. Four females killed later were not. This difference was significant (Fisher's exact test, two-tailed P<0.05). Five males, all without a female within their territory, left their territories. One left in mid-February; the others left in late March and early

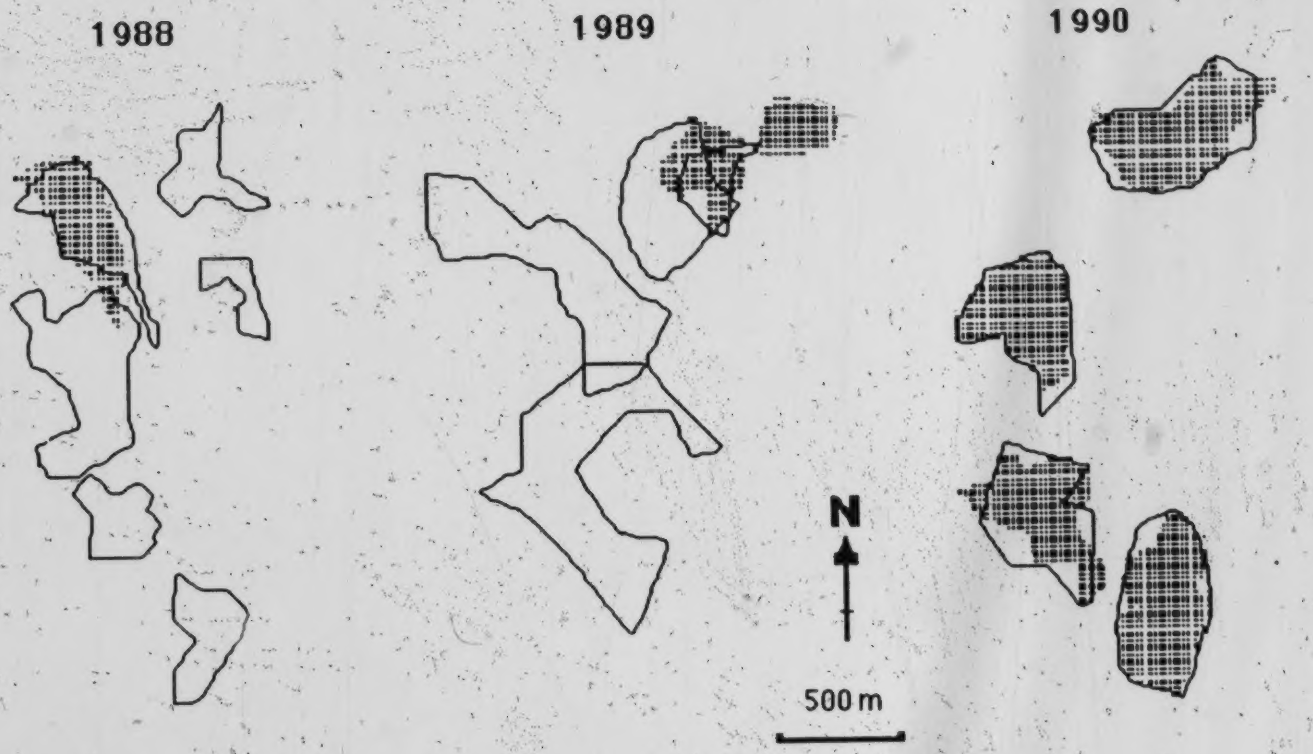

Fig. II-1. Overlap of territories of radio-marked male (lines) and female (shaded) hazel grouse during the breeding season.

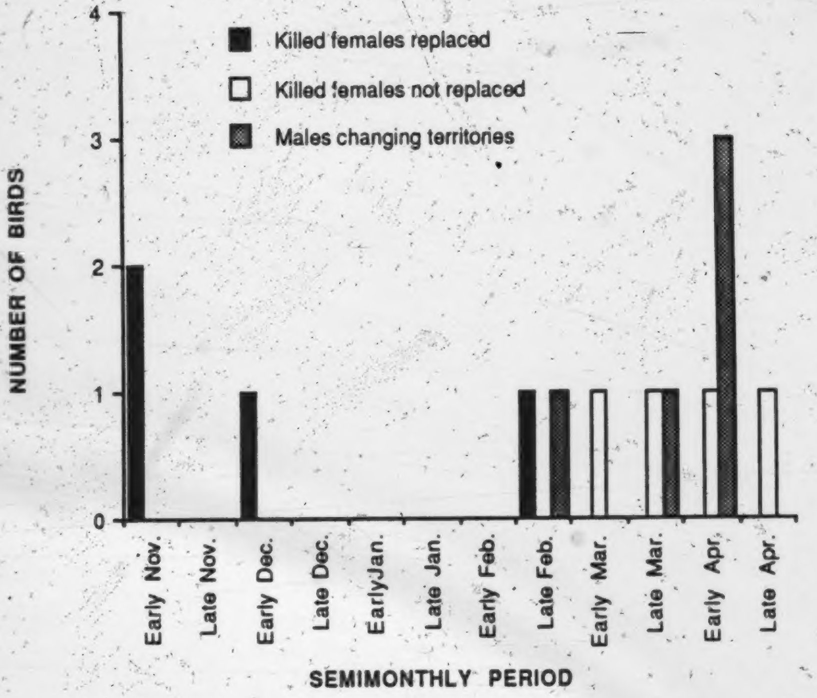

Fig. II-2. Whether or not radio-marked territorial female hazel grouse were replaced on territories by the next breeding season relative to the time they were killed and timing of leaving territories by radio-marked male hazel grouse in the spring.

April (Fig. II-2) and moved a minimum of 2.1-14.3 km, but both radio-marked survivors returned in early to mid-September to their original territories. At least one of these males established a new territory in the spring and was with a female on it. Two males without females in their territories did not leave; one was with a female during the relaying receptive period.

Mating tactics

During the prelaying receptive period, four of nine females were known to have been with two males, and during the renesting receptive period, two of 10 females were with two males and one was with three males (Table II-1). Combining these periods, a maximum of 63% of the females were monogamous during a given receptive period. All females shared their territory with a male; other males they visited probably were neighboring males, although some unmarked males may have been transients.

Males may have had few opportunities to gain multiple matings (Table II-1). Two of 15 males never were seen with a female during the prelaying period and one was seen with two females. During the renesting period, four of 16 males were never seen with a female and none was seen with >1 female. In combination, a maximum of 77% of the males were monogamous during a given receptive period, 19% were not with a female, and only 3% were with two females. During a receptive period, 37% of 19 females were documented in escort of more than one male, but only 3% of 30 males were known to be with more than one female (χ^2_c=7.56, df=1, P=0.006).

Only one of the males followed through both prelaying and renesting receptive periods was never seen with a female. Some females were with different males in the prelaying and renesting receptive periods. During the three breeding seasons of study, only two of 13 females successfully hatched their first clutch. Therefore, there were almost as many females available during the renesting period as the prelaying period. In 1990, all males and females were observed with only one individual of the opposite sex (Table II-1). This was also the year with the lowest population density.

The sex ratio appeared to be male biased (Table II-2), with an average of 1.2 territorial males per territorial female on 1 May. Including males that left the study area prior to 1 May, this value rose to 1.4 males per female. The latter estimate was probably more accurate, because it included transient males, assuming that as many males entered the area as left it. This sex ratio was not significantly different from 50:50 (one group χ^2=1.2, df=1, P=0.27), but this may have been due to the low sample size; the area was surveyed intensively and the majority of the territorial birds were radio-marked.

During the 1989 prelaying period, the territories of two males and one female overlapped. Male 384 and female 390 were captured in 1988 and by spring 1989 both were ≥3 years old; male 397, captured in spring 1989, was a yearling. Male 384 (375 g) weighed 10% more than male 397 (341 g). During early spring, no female occupied male 384's territory, and it made some excursions outside of the territory, up to 1 km. On about 18 April, male 384 moved to overlap 43% of female 390's territory and 32% of male 397's territory.

Table II-1. Number of birds of the opposite sex with hazel grouse during the prelaying and relaying receptive periods.

			Number of escorts of opposite sex						
		Pop.	Prelaying[b]			Renesting[c]			
Category	Year	density[a]	0	1	2	0	1	2	3
Females	1988	4.61	0	1	1	0	1	1	0
	1989	2.56	0	0	3	0	2	1	1
	1990	2.05	0	4	0	0	4	0	0
	Total		0	5	4	0	7	2	1
Males	1988	4.61	0	6	0	1	4	0	0
	1989	2.56	2	2	1	3	4	0	0
	1990	2.05	0	4	0	0	4	0	0
	Total		2	12	1	4	12	0	0

[a] Males per 100 ha on the study area; whistle surveys (Swenson 1991).
[b] From 1 May to start of incubation, usually about 15 May.
[c] From loss of nest to 15 June.

Table II-2. Sex ratio of hazel grouse on the study area on 1 May. (The area covered varied somewhat from year to year, depending on where the radio-marked grouse were located, which determined where the number of unmarked territorial grouse could be accurately estimated.)

Category	Year	Males	Females	Total	Males per 100 females
Without emigrants	1988	8	7	15	114
	1989	7	4	11	175
	1990	6	6	12	100
	Total	21	17	38	124
With emigrants	1988	8	7	15	114
	1989	8	4	12	200
	1990	8	6	14	133
	Total	24	17	41	141

Despite the overlap, males 384 and 397 were never observed or relocated together, yet on several occasions one was heard answering the territorial advertisement of the other. Female 390 was with both males during the prelaying receptive period; ≤20 m from male 384 during 38% of 21 relocations, 19% with male 397, and 43% alone. Sometimes the female moved rapidly from one male to the other, for example, on 11 May (during egg laying): at 0720 hours, 390 was with 397 and 384 was 165 m away, 17 minutes later, 390 was with 384 and 397 was 95 m away. Female 390 began incubating sometime during 14-19 May, and male 397 left the area during 20-22 May, but male 384 stayed. Female 390 was with male 384 and an unmarked male during the renesting period also.

Comparison of spring and autumn territoriality

Several behavioral patterns varied throughout the year, with distinct differences between the spring and autumn when territorial behavior is most pronounced. In both autumn and spring, hazel grouse showed peaks in response to an imitated territorial song, but only in spring did they show a peak in spontaneous advertisement (Fig. II-3). The incidence of border disputes was higher in autumn than in spring for both males and females (Fig. II-4). Females were generally more active than males throughout the year, but this pattern was most apparent during February through April (Fig. II-5). Although females were more active than males in spring, males were generally more mobile (Fig. II-6). Females moved somewhat more than males in autumn and somewhat less than males in spring.

Hazel grouse males responded more quickly to an imitated territorial song in the spring (2.49±0.15 min, N=152) than in autumn (3.68±0.16, N=206) (Swenson 1991). In addition, responding hazel grouse males sang more often in spring (84%) than in autumn (52%), when wing-produced sounds were more common (Swenson 1991). However, when advertising spontaneously in autumn, song was most common, 66% of the instances recorded, followed by flutter jumps, 21%, and flutter flights, 14% (N=29). This was different from that recorded in spring; 35% songs, 54% flutter jumps, and 11% flutter flights (N=114, $\underline{X}^2$=10.61, df=2, two-tailed P=0.005).

DISCUSSION

Social organization

From the standpoint of social organization, most hazel grouse in this study were clearly monogamous; the pair was the social unit. Scherzinger (1981) reached the same conclusion, based on a study of the behavior and vocalizations of captive hazel grouse. Both males and females defended territories from members of the same sex, but pairs were together more than expected by chance and shared the same space. Even in the instance where an older and larger male intruded into the territory of a yearling male so that the territories overlapped an average of 32%, the single female in the territory was never with both males at the same time. The social organization in spring was very similar to that in the autumn and winter, with defended territories and a one

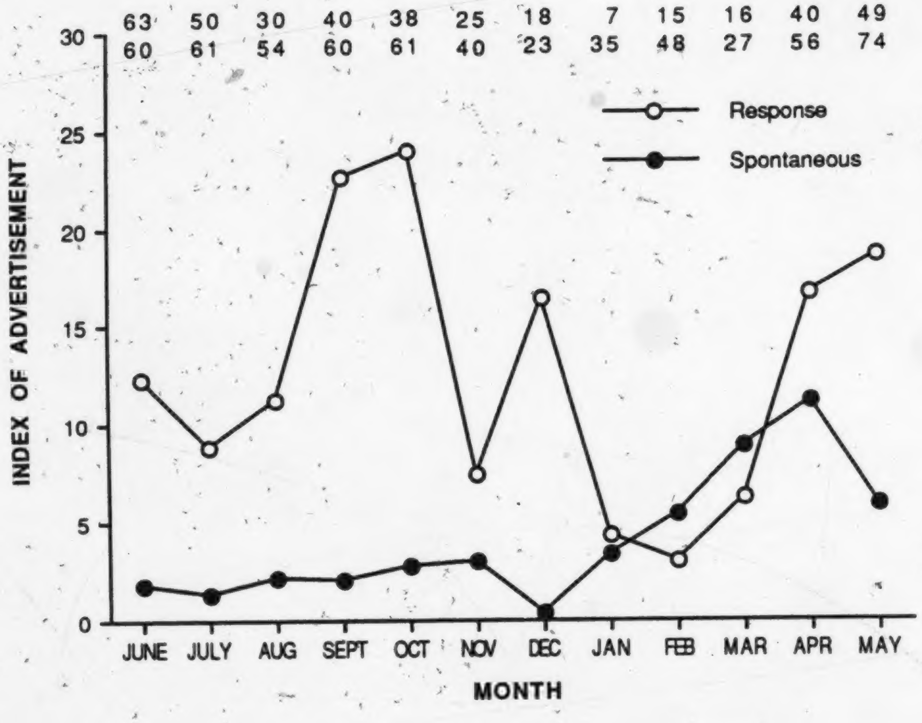

Fig. II-3. Monthly indices of spontaneous territorial advertisement on the study area (instances per 10 field days) and of responses to an imitation of the territorial song (instances per 5 field days) in southern Finland (from Pynnönen 1954:69). Numbers are field days for response (above) and spontaneous data (below).

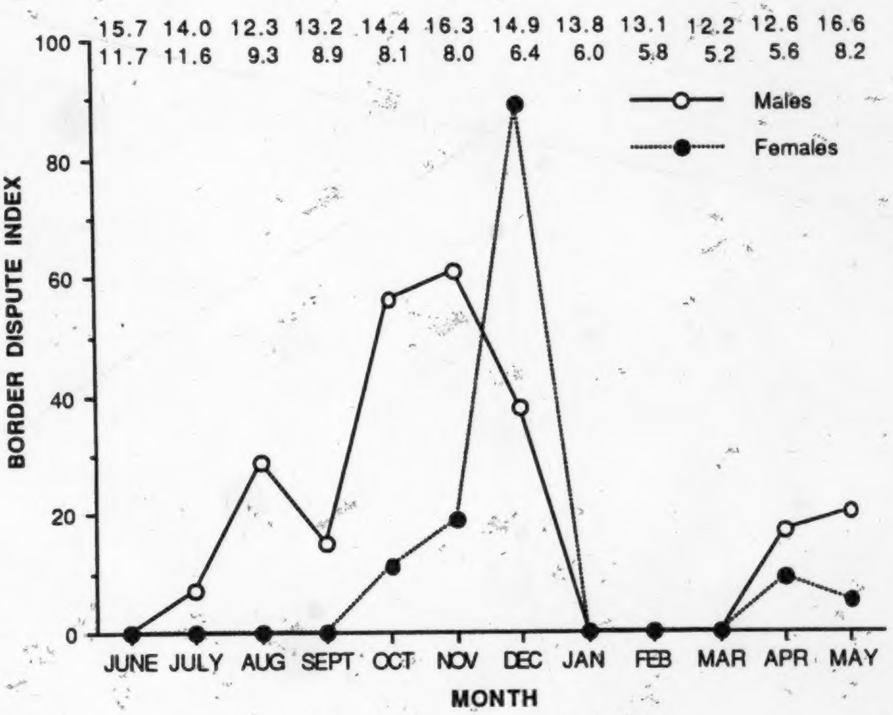

Fig. II-4. Monthly indices of border disputes by radio-marked male and female hazel grouse on the study area. (Indices were the number of border disputes divided by the product of radio-marked birds of each sex available that month times the number of months in the field [days÷30].) Numbers are this product for males (above) and females (below).

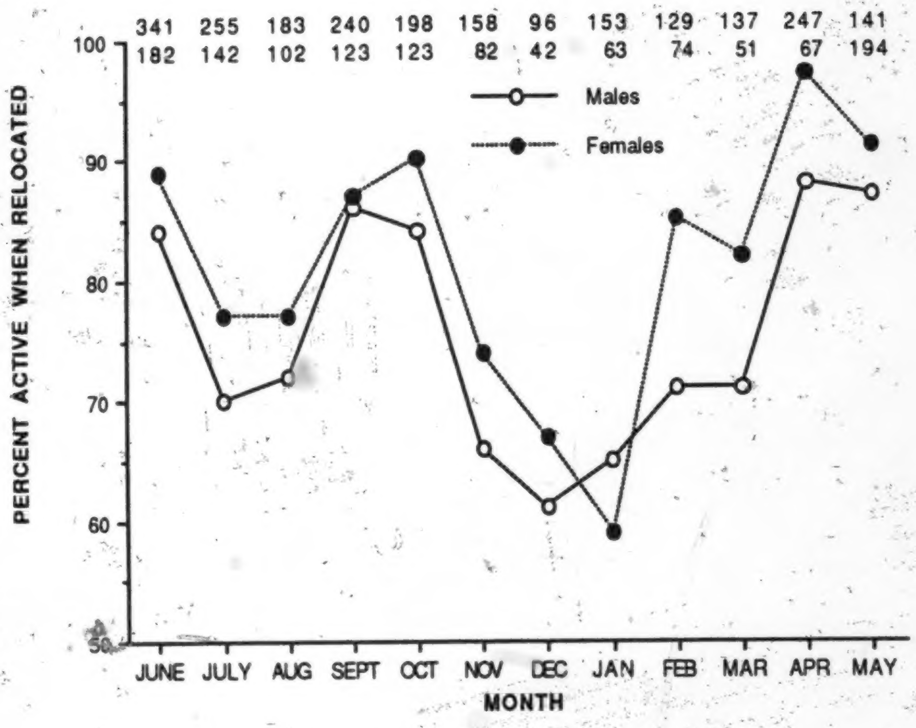

Fig. II-5. Monthly indices of activity of radio-marked male and female hazel grouse on the study area. Numbers are sample sizes for males (above) and females (below).

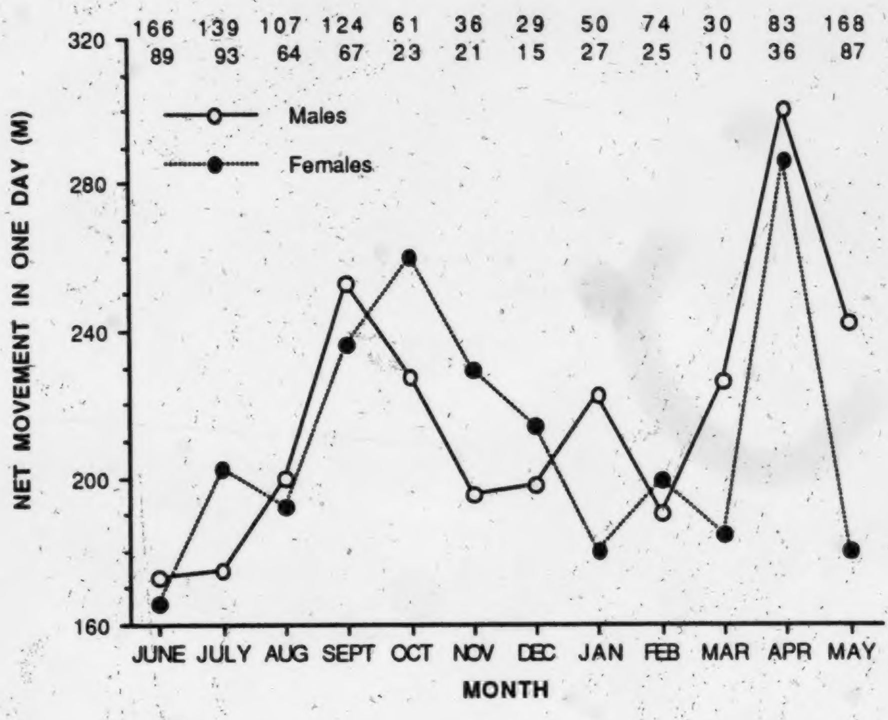

Fig. II-6. Monthly rates of movement of radio-marked male and female hazel grouse on the study area. Movement rate was the mean distance between relocations on two consecutive days. Numbers are sample sizes for males (above) and females (below).

male-one female social unit, except that the members of a pair did not share the same space in autumn and winter (Chapters IV and V). The correlation between territory size and density suggested that intruder pressure was one factor limiting territory size in both sexes (Hixon 1987).

Based on my results, I am not able to explain the observations of more than one female with a male in spring reported by Pynnönen (1954) and Ivanter (1962). Both authors studied very dense populations of hazel grouse and remarked that such observations were rare. Perhaps they observed females at the boundaries of their territories, what I termed a territory dispute (Fig. II-4), when only one male was present. Sugimoto (1986) attempted to mate hazel grouse polygynously, with one male and four females in a 20.4 m^2 cage, and monogamously, in 6 and 10 m^2 cages. Both monogamous females laid fertile eggs, but, although all the polygynous females laid eggs, only one laid fertile eggs. Sugimoto (1986) attributed this to females chasing each other, and suggested that this behavior prevented polygyny.

Behavior of males and females was more similar during the nonbreeding season (Chapter IV) than the breeding season, although both sexes showed a reduction in border disputes in spring (Fig II-4), perhaps because of a lower population density then. Females were more active than males in spring, compared with autumn (Fig. II-5), but females were less mobile than males in spring, opposite to the pattern observed in autumn (Fig. II-6). The behavior differed between males and females during spring. Perhaps females were spending more time foraging (greater activity) whereas males were spending more time patrolling for intruding males and looking for females (greater mobility). This was also suggested by the difference in temporal patterns of changing territories (Fig. II-2). Females were not observed changing a territory after late February, suggesting that they were bound to their prelaying territories after that date. Unpaired males that left their territories did so later, after females had stopped changing territories. Pynnönen (1954) arrived at the same conclusion, although he did not study marked birds. At least one of these males that moved established a new territory with a female. All three radio-marked males that left in spring and survived to autumn returned to their original territory the following autumn (two unpaired males and male 397).

Males reacted significantly more aggressively to an imitation of the territorial song in spring than autumn (Swenson 1991) and advertised spontaneously more often (Fig. II-3). The difference in type of advertisement suggested a difference in behavior in spring and autumn. Song was used by both sexes as a contact sound (Chapter VI), and the flutter jump could be used to communicate with rivals or to warn the other member of the pair of danger (Scherzinger 1981, pers. obs.). This ambivalence made it difficult to interpret differences between spring and autumn. The increased spontaneous advertisement in spring (Fig. II-3) may have been due to a combination of increased contact sounds between the pair, increased advertisement by nearby territorial males, and perhaps calling for a female by transient males. The increased use of spontaneous wing-produced sounds in spring appeared to be predator warnings, provided particularly by the male to the female, based on several instances when I unexpectedly came upon a pair.

Mating system

Although social organization is a characteristic of a group of individuals, mating system refers to individual tactics (Wickler & Seibt 1983). The data indicated that male and female hazel grouse pursued different mating tactics. Monogamy apparently was the dominant mating tactic among both male and female hazel grouse, but polygamy, particularly polyandry, may also have been common although it has not been reported in the literature previously (Pynnönen 1954, Ivanter 1962, Dement'ev et al. 1967, Hjorth 1970, Glutz von Blotzheim et al. 1973, Scherzinger 1981, Bergmann et al. 1982, Potapov 1985).

Females did not change territories during the prelaying period and, although all shared a territory with a male, at least 37% were potentially polyandrous during a given receptive period. This was a minimum estimate because the dense vegetation on the study area and the secretive nature of hazel grouse made observations difficult. Several factors contributed to the potential for polyandry: 1) an apparently male-biased sex ratio (40% more males than females, Table II-2), 2) attentive neighboring males, both with and without females on their territories, and 3) the movement of some unpaired males from their territories, presumably in search of females. A male-biased sex ratio is apparently common in hazel grouse populations, as it has been documented also in European Russia (Gaidar 1974, Ivanter 1962) and Siberia (Chapter VI). Moreover, unpaired males have been reported often (Hjorth 1970, Pynnönen 1954, Tomek 1965, Wiesner et al. 1977) and Pynnönen (1954) reported wandering males in the spring. Emlen & Oring (1977) have shown how a male-biased sex ratio and highly synchronous nesting can promote monogamous mating. Nesting was synchronous on the study area, as incubation began at first nests of marked females within a five-day period each year. Renesting, however, was not synchronized.

Males defended territories from other males during the spring, as during autumn and winter (Chapter IV). However, they appeared to leave their territories more readily than females in spring. A limiting resource for males appeared to be a relative lack of females; implying that an important function of the spring territory was to provide access to a female. Males apparently had few opportunities to be polygynous (minimum of 3%), because they were faced with a strongly male-biased sex ratio (Table II-2) and stationary females that did not change territories after early March (Fig. II-2). The difficulties of observing a male with a female were the same as observing a female with a male. Therefore, although both estimates were minimal, they had a similar bias. Males appeared to use alternate mating tactics depending on whether they shared a territory with a female. All males that shared a territory with a female stayed with that female (N=11). Males without a female showed three tactics: 1) they stayed on their territory but used twice as much space as males with a female, apparently to try to gain matings with a neighboring female (N=2), 2) they left their territories (N=5), usually after 15 March, when females stopped changing territories, moved 2.1-14.3 km and returned in the autumn; this tactic was successful in at least one instance, or 3) they moved into a neighboring male's territory to share the female. This was recorded once, when a ≥3-year-old male that was 10% heavier than a neighboring yearling male moved into the yearling's territory. After the female nested, the yearling left the territory but the adult stayed.

It was surprising that unpaired males were adults that had bred previously and had territories twice as large as paired males. In willow ptarmigan, unpaired males are more often yearlings and have smaller territories than paired males (Hannon 1983, Pedersen 1984, Moss et al. 1988). The unpaired males were both ≥3 years old and both lost the female on their territory in early April with no replacement female appearing. The lack of a female on the territory apparently affected the male's behavior. Perhaps they doubled their use of space searching for another female. One of these males succeeded in being with an unmarked female once during the renesting period. This occurred at the edge of the male's territory, and the female was probably from the neighboring territory.

Females accepted the company of the male in the same territory, neighboring males, and transient males, and presumably had the opportunity to mate with any of them. For example, female 390 was with both the smaller, yearling male 397 and the larger, ≥3-year-old male 384 on the same territory. Also, Hjorth (1970) reported an experiment in which five male hazel grouse were shot sequentially from the territory of one female. Females appear to establish their own territories, rather than choose those of males, and females that have the opportunity to mate with more than one male may do so as a bet-hedging tactic to obtain offspring with genes from more than one male (Oring 1982).

Monogamy in hazel grouse

Are hazel grouse monogamous? The social unit was monogamous: no more than one male and one female were seen together at one time. This confirms the results of earlier studies with captive and unmarked wild birds (Donaurov 1947, Pynnönen 1954, Ivanter 1962, Scherzinger 1981). However, the mating tactics varied between and within sexes, particularly among females. Most males were monogamous, but at least 37% of the females had the opportunity to be polyandrous. The pair bond in hazel grouse appeared to be much weaker than in willow ptarmigan. In hazel grouse, the pairs were together 37±5% of the time during prelaying, compared to 90% for willow ptarmigan (Hannon & Martin in press). Mating systems are difficult to classify because they lie on a continuum from polygyny to monogamy to polyandry (Barlow 1988). This hazel grouse population appeared to have a mating system that was close to monogamy, but may have been on the polyandrous side of it on this continuum. Brander (1967) reported that female ruffed grouse (Bonasa umbellus) visited several males during the breeding season, but had no information on how many females visited a given male.

Although not documented, this study provides the first suggestion of a potentially polyandrous mating system within the subfamily Tetraoninae (Vos

1979, Hjorth 1970, Wittenberger 1978, Wiley 1974). This possibility should be investigated using genetic markers to determine how many of the young are fathered by the "primary" male in a female's territory.

LITERATURE CITED

Alatalo, R. V., L. Gustafsson & A. Lundberg. 1984. High frequency of cuckoldry in pied and collared flycatchers. Oikos 42:41-47.

Barlow, G. W. 1988. Monogamy in relation to resources. Pp. 55-79 in C. N. Slobodchikoff, ed. The ecology of social behavior. Academic Press, Inc., New York.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn, Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Björklund, M. & B. Westman. 1983. Extra-pair copulations in the pied flycatcher (Ficedula hypoleuca): a removal experiment. Behav. Ecol. Sociobiol. 13:271-275.

Björklund, M. & B. Westman. 1986. Mate-guarding in the great tit: tactics of a territorial forest-living species. Ornis Scand. 17:99-105.

Brander, R. B. 1967. Movements of female ruffed grouse during the mating season. Wilson Bull. 79:28-36.

Brodsky, L. M. 1988. Mating tactics of male rock ptarmigan, Lagopus mutus: a conditional mating strategy. Anim. Behav. 36:335-342.

Dement'ev, G. P., N. A. Gladkov, Yu. A. Isakov, N. N. Kartashev, S. V. Kirikov, A. V. Mikheev & E. S. Ptushenko. 1967. Birds of the Soviet Union, Vol. 4. U.S. Dep. Inter. & Nat. Sci. Found., Washington, D.C.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika 4:77-122. (In Russian)

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Gardarsson, A. 1988. Cyclic population changes and some related events in rock ptarmigan in Iceland. Pp. 300-329 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Gaidar, A. A. 1974. Dinamika chslennosti i puti ratsional'nogo osvoeniya zapasov ryabchika. Sbornik Nauchno-tekhn. Inform. Kirov 44/45:47-51. (In Russian)

Glutz von Blotzheim, U. N., K. M. Bauer & E. Bezzel. 1973. Handbuch der Vögel Mitteleuropas. Vol. 5, Galliformes und Gruiformes. Akademische Verlagsgesellschaft, Frankfurt am Main.

Gowaty, P. A. 1985. Multiple parentage and apparent monogamy in birds. Ornithol. Monogr. 37:11-21.

Gowaty, P. A. & A. A. Karlin. 1984. Multiple paternity and maternity in single broods of apparently monogamous eastern bluebirds. Behav. Ecol. Sociobiol. 15:91-95.

Haga, R. & S. Takamata. 1986. Ecology and breeding biology of hazel grouse Tetrastes bonasia in captivity. 1. Breeding, artificial insemination (sic. incubation), and rearing control. Tori 34:105-125. (In Japanese, English summ.)

Hannon, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alternation of sex ratio. J. Anim. Ecol. 52:807-820.

Hannon, S. J. & K. Martin. In press. Monogamy in willow ptarmigan: is male vigilance necessary for reproductive success and survival of females? Anim. Behav.

Harvey, M. J. & R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum home range method. J. Mammal. 46:398-402.

Hixon, M. A. 1987. Territory area as a determinant of mating systems. Am. Zool. 27:229-247.

Hjorth, I. 1970. Reproductive behaviour in Tetraonidae, with special reference to males. Viltrevy 7:183-596.

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In Russian)

Johnsgard, P. A. 1983. The grouse of the world. Univ. Nebraska Press, Lincoln.

Kenward, R. 1987. Wildlife radio tagging, equipment, field techniques and data analysis. Academic Press, London.

Martin, K. & S. J. Hannon. 1988. Early pair and extra-pair copulations in willow ptarmigan. Condor 90:245-246.

McKinney, F., K. M. Cheng & D. J. Bruggers. 1984. Sperm competition in apparently monogamous birds. Pp. 523-545 in R. L. Smith, ed. Sperm competition and the evolution of animal mating systems. Academic Press, Inc., New York.

Moss, R., A. Watson & R. Parr. 1988. Mate choice by hen red grouse Lagopus lagopus with an excess of cocks--role of territory size and food quality. Ibis 130:545-552.

Oring, L. W. 1982. Avian mating systems. Avian Biol. 6:1-92.

Parker, H. 1981. Duration of fertility in willow ptarmigan hens after separation from the cock. Ornis Scand. 12:186-187.

Parker, H., H. Mjelstad & J. T. Solheim. 1989. Duration of fertility in capercaillie hens after separation from males. Ornis Scand. 20:307-310.

Pedersen, H. C. 1984. Territory size, mating status, and individual survival of males in a fluctuating population of willow ptarmigan. Ornis Scand. 15:197-203.

Potapov, R. L. 1985. Fauna SSSR, ptitsy, otryad kyroobraznye (Galliformes), semeistvo teterevinye (Tetraonidae). Nauka, Leningrad. (In Russian)

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Scherzinger, W. 1981. Stimminventar und Fortpflanzungsverhalten des Haselhuhnes Bonasa bonasia. Ornithol. Beob. 78:57-86.

Semenov-Tyan-Shanskii, O. 1959. Ekologiya teterevinykh ptits. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1-318. (In Russian)

Stenman, O. & M. Helminen. 1974. Aging method of hazel grouse (Tetrastes bonasis) based on wings. Suomen Riista 25:90-96. (In Finnish, English summ.)

Sugimoto, M. 1986. Captive breeding and behavioral analysis of hazel grouse Tetrastes bonasia. Thesis, Obihiro Univ. Agr. Vet. Med., Obihiro, Japan.

Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse Bonasa bonasia in spring and autumn. Ornis Fennica 68: in press.

Tomek, W. 1965. Hazel hen in Ciezkowice Highlands, southern Poland. Przeglad Zool. 9:395-404. (In Polish, English summ.)

Unander, S. & J. B. Steen. 1985. Behaviour and social structure in Svalbard rock ptarmigan Lagopus mutus hyperboreus. Ornis Scand. 16:198-204.

Vinokurov, A. A. 1983. Comparative aspects of rock ptarmigan and willow ptarmigan biology in typical tundras of Taimyr. Proc. Congr. Intern. Union Game Biol. 16:711-715.

Vos, G. J. de. 1979. Adaptedness of arena behaviour in black grouse (Tetrao tetrix) and other grouse species (Tetraoninae). Behaviour 68:277-314.

Wang, X., N. Liu, Y. Chen, Y. Yang & M. Xu. 1987. Ecological studies of the Chinese hazel grouse (Tetrastes s. sewerzowi). Acta Zool. Sinica 33:73-81. (In Chinese, English summ.)

Wickler, W. & U. Seibt. 1983. Monogamy: an ambiguous concept. Pp. 33-50 in P. Bateson, ed. Mate choice. Cambridge Univ. Press, Cambridge.

Wiesner, J., H.-H. Bergmann, S. Klaus & F. Müller. 1977. Siedlungsdichte und Habitatstruktur des Haselhuhns (Bonasa bonasia) im Waldgebiet von Bialowieza (Polen). J. Ornithol. 118:1-20.

Wiley, R. H. 1974. Evolution of social organization and life-history patterns amoung grouse. Quart. Rev. Biol. 49:201-227.

Wittenberger, J. F. 1978. The evolution of mating systems in grouse. Condor 80:126-137.

III. FACTORS PROMOTING FEMALE TERRITORIALITY AND MONOGAMY IN HAZEL GROUSE

INTRODUCTION

Monogamy is the dominant mating system among birds (Lack 1968), but it has recieved less attention from researchers than other avian mating systems (Mock 1985), and only recently has an explicit theory of the evolution of monogamy been developed (Kleiman 1977, Wittenberger 1979, Wittenberger & Tilson 1980). Historically, the necessity of male parental care to produce offspring has been offered as a major factor promoting monogamy in birds (Lack 1968), although it is now evident that the value of male parental care varies among species (Dunn & Hannon 1989). Wittenberger & Tilson (1980) have presented alternative hypotheses that include species with no male parental care and that assume females select males and the resources on their territories. In this case, a female may choose monogamy if its reproductive potential is increased by pairing with an unmated male rather than with a male that is already mated, and thereby having to share its attention and the resources on its territory with another female (the polygyny-threshhold hypothesis, Verner & Willson 1966, Orians 1969). However, even if the polygyny threshhold is exceeded, polygyny can be prevented if aggression by mated females prevents males from acquiring additional mates (Wittenberger & Tilson 1980).

The range and gradations of social organization and mating systems among the grouse (subfamily Tetraoninae) are among the greatest within an avian subfamily (Wiley 1974). As grouse are also a closely related group (Short 1967), they provide an excellent opportunity to compare the factors affecting the evolution and maintenance of various mating systems. Studies of monogamy in grouse have been limited to ptarmigan, particularly the willow ptarmigan (Lagopus lagopus). In that genus, females settle on male territories (Bergerud & Mossop 1984), fulfilling an important assumption of the hypothesis of Wittenberger & Tilson (1980), namely that females choose males on a territory. Female willow ptarmigan also defend exclusive territories against other females during the prelaying and laying periods (Hannon 1983).

Female hazel grouse (Bonasa bonasia) also exhibit intrasexual aggressiveness and defend territories, but females appear to select their own territories and males appear to move onto female territories during the breeding season (Chapters II & IV). Thus, because females do not appear to settle in male territories, hazel grouse do not fit well into the hypothetical framework provided by Wittenberger & Tilson (1980). Also, the mating tactic of individual females appeared variable; monogamy was most common, but many females had the opportunity to mate polyandrously (Chapter II). Fortunately, the social and mating systems of hazel grouse allowed independent testing of hypotheses about factors promoting female territoriality and monogamy.

Three major hypotheses dealing with female territoriality and/or aggressiveness in spring are: 1) the territory is defended to secure food resources for the prelaying female, presumably an energy maximizer at this time (Schoener 1971, Wittenberger 1978, Savard 1988, Naylor & Bendell 1989), 2) territoriality spaces nests to reduce nest predation (Nugent & Boag 1982, Bergerud & Gratson 1988), and 3) females may be guarding their nests to prevent intraspecific egg parasitism (Gowaty et al. 1989). The latter hypothesis does not necessarily predict female territoriality; intrasexual aggresssion and attendence at the nest may be sufficient.

An important assumption of the food hypothesis is that females have a significant nutritional demand during the spring. Predictions arising from the food hypothesis include the following: 1) territories will be centered on areas with adequate spring food, 2) there will be an inverse relationship between territory size and both food abundance and competitor density (Gauthier 1987, Hixon 1987), 3) positive relationships will exist between food abundance and clutch size (Naylor & Bendell 1989) and between clutch size and egg size, because females on a higher plane of nutrition produce both more and larger eggs (Savory 1975, Högstedt 1981, Beckerton & Middelton 1982), 4) timing of reproduction will be related to plant phenology (Lack 1968, Siivonen 1957), and 5) reproductive success will be positively related to food abundance on the territory (MacLean & Seastedt 1979, Gauthier 1987). It was not possible to test the last prediction during this study, because of high nest predation and clutch removal experiments.

The nest dispersion hypothesis predicts that nests will be maximally dispersed to reduce the probability of depredation (Bergerud & Gratson 1988); if female territories are contiguous, nests should be located centrally within the territories. The nest guarding hypothesis predicts that females will remain closer to their nests during than before laying (Gowaty et al. 1989).

Male grouse do not provide parental care, except in willow ptarmigan. Even in willow ptarmigan, male parental care does not appear to be an important factor maintaining monogamy (Hannon 1984, Martin & Cooke 1987, Hannon & Martin in press). Other factors postulated to promote monogamy include the following: 1) males serve a sentry function, providing vigilance against predators (Wittenberger 1978, Bergerud & Gratson 1988), 2) males are mate guarding to prevent extra-pair copulations with their mates (Björklund & Westman 1986, Brodsky 1988, Gowaty et al. 1989), and 3) demography; a male-biased operational sex ratio and highly synchronous breeding will promote monogamy (Emlen & Oring 1977).

Under the male sentry hypothesis, an assumption is made that females, while foraging intensively, are vulnerable to predators. There should be an abrupt decrease in distance between the birds when the females begin to be stressed for time and/or nutrition while foraging in the spring, but males should remain as close to females during the nonfertile periods when the females forage intensively as during the fertile period (Wittenberger 1978, Björklund & Westman 1986, Gowaty et al. 1989). As territory security varied greatly on the study area, the male sentry hypothesis also predicts that intrapair distances will be inversely related to territory security, and that monogamous females will be more prevalent in the less secure territories. The survival rate of radio-marked hazel grouse was used as an index of territory security (see Chapter VIII).

The mate guarding hypothesis predicts that intrapair distances will decrease abruptly when the female enters her fertile period (Björklund & Westman 1986, Gowaty et al. 1989). No relationship between intrapair distance and territory security is expected. The demography hypothesis predicts a male-biased operational sex ratio and highly synchronous breeding.

STUDY AREA AND METHODS

The study area (285 ha, 195 ha of forest) was within a forest reserve on the Grimsö Wildlife Research Area in southcentral Sweden (59-60° N and 15-16° E). It is described in detail in Chapter VII.

The study encompassed three breeding seasons, 1988 through 1990, and made use of radiotelemetry. Hazel grouse were captured in spring and autumn by luring or chasing them into nylon fishing nets. They received ca. 16-g necklace-type transmitters (Kenward 1987) that weighed ca. 4.5% of the birds' weight. Age was determined by the coloration of primary feather P1 (Stenman & Helminen 1974) and birds were classified as either yearlings or adults. When captured, the birds were weighed to the nearest 10 g with a Pesola 500 g spring scale; net weight was determined by subtracting the estimated weight of crop contents, as determined from weighing crop contents of dead birds (Comeau & Keppie 1989).

Size and location of territories were determined each season for birds with 25 or more relocations, using the method of Harvey & Barbour (1965). Most relocations were based on three bearings, or two if the bird was within 100-150 m. Relocations were accurate; 75% were ≤20 m of the actual location (Chapter IV). Territory size was measured from a 1:15,000 map with a Kempten planimeter.

Abundance of spring food was determined by vegetation surveys conducted in summer. Coverage of forbs and cottongrass (Eriophorum vaginatum and E. angustifolium) were estimated to the nearest 10% on 566 plots, 10 m in radius, located systematically over the entire study area at a density of two per ha. In this chapter, the term "forbs" refers to Viola spp., Anemone nemorosa, Oxalis acetosella, and Potentilla erecta, which are important spring foods of hazel grouse (Ahnlund & Helander 1975). Feces were collected in spring 1988 and the proportion of forbs and cottongrass in them were estimated visually.

Pairs were defined as a territorial male and female with territories that overlapped more than 50% and that were together more than either was with birds of the opposite sex during the breeding period. The term pair did not imply exclusive mating. During the breeding season, radio-marked birds were relocated 5-15 times a week and males and females that were not relocated with another marked bird were approached as often as possible (50-75% of the instances) to determine if they were with an unmarked bird. No copulations were observed during this study, but it was assumed that all observations of a male and female together during the receptive periods could have resulted in a copulation, which was probably a reasonable assumption (see Chapter II). All spontaneous advertising (vocaliztions and wing-produced sounds) heard in the field was recorded.

The prebreeding and breeding seasons were divided into several periods, based on the behavior of the females. The period when males and females were relatively sedentary began arbitrarily on 1 January and lasted until 31 January (Chapter II). Female activity increased from 1 February and lasted until 37 days before laying; this was termed the female activity period. The cutoff of 37 days before laying was determined a posteriori, based on data on body mass. A period of female weight gain lasted from 36 to 9 days before laying. Females probably were not fertile at this time (Chapter II). The fertile period lasted from 8 days before laying to the start of incubation (see Chapter II). These periods were determined individually for each female, and if killed before laying, the mean date of laying for that year and mean clutch size were used. Survival during breeding periods was calculated from a daily survival rate of radio-marked birds (Trent & Rongstad 1974).

Distance from the first nest site was determined for locations of females during laying and during the 10 days before the onset of laying. Maxson (1977) reported that three intensively monitored female ruffed grouse (Bonasa umbellus) visited their nest sites 9-13 days before initiating laying.

Hazel grouse were counted within 66 forest stands 26±0.6 (SE) ha in size in the industrial forest of Grimsö Wildlife Research Station during 1988-1990. Each stand was censused during two springs and two autumns using the method described in Swenson (1991). The soil productivity of each stand was classified into 10 categories based on field vegetation, and the categories were ranked from richest to poorest following Hägglund & Lundmark (1984).

Eggs from the study area and the bordering provinces, from museums at Uppsala University, the National Museum, and a private collection, were measured to the nearest 0.1 mm with calipers. Only eggs from clutches of known size and with not more than one missing egg were used. Fresh eggs from Grimsö were weighed to the nearest 0.01 g on a Sartorius balance. Data on egg size in clutches of different size from a Japanese study (Haga & Takamata 1986) were also analyzed.

The dispersion pattern of spring foods was tested against randomness (a Poisson distribution), using a one-group X^2 test. If different from randomness, dispersion was regular if the variance:mean ratio was less than 1.0, and clumped if it was greater than 1.0 (Zar 1974). The standard error of the mean is presented with means. Unless otherwise stated, tests are one-tailed, as specific predictions were tested. A probability of 0.05 was accepted as the limit for rejecting a null hypothesis.

RESULTS

During the three breeding seasons of this study, 11 marked females were followed for 12 seasons, and 10 marked males were followed for 16 seasons; 60-100% of the males and 33-100% of females on the study area were radio-marked each breeding season. However, gathering data on pairs was hampered by female mortality and transmitter failures (3) during the breeding season, although all birds with failed transmitters were eventually recaptured during spring.

Factors promoting female territoriality and aggression

Food shortage hypothesis. Females had a significant nutritional demand in late spring before laying. Net body mass of females increased rapidly from 36 days before laying to the onset of laying (r^2=0.66, df=7, two-tailed P=0.008, Fig. III-1). Based on the formula, body mass = 444.7 - 2.432 · (number of days before laying), I calculated that females gained 88 g in mass, or 25% of their initial weight, during the 36 days before laying. Males, however, showed no change in body mass during the same period (r^2=0.005, df=14, two-tailed P=0.79, Fig. III-1). During early spring (21 March to 15 April), the body mass of males (359±6 g, N=6) was similar to that of females (363±8 g, N=6, Mann-Whitney test, U=19.5, df= 11, two-tailed P=0.81). However, after 15 April and up to laying, females were heavier (421±13 g, N=5) than males (347±7 g, N=9, U=45, df=13, two-tailed P=0.003).

The censuses of forest stands revealed that hazel grouse selected rich sites for their territories. Site productivity was higher in stands where hazel grouse were found than those without hazel grouse (U=721.5, df=65, P=0.005). Further, stands occupied by hazel grouse in spring were richer than those with hazel grouse only in autumn (U=166, df=27, P=0.0006).

During the prelaying period, hazel grouse at Grimsö foraged on both newly sprouted forbs and the inflorescenses of cottongrass. An analysis of 42 droppings from seven territories in 1988 showed an average of 79% forbs and 21% cottongrass, but the method may have overrepresented cottongrass, because of the abundance of the undigested bracts in the feces. The mean proportion of forbs in the droppings from each territory was positively correlated with the density of forbs within each territory (Spearman rank correlation, r_s=0.739, df=5, P=0.035). The corresponding relationship for cottongrass was suggestive (r_s=0.505, df=5, P=0.108). The proportion of forbs in the droppings from each territory was higher than that expected based on the relationship of forb and cottongrass densities within the territories (Wilcoxon signed rank test, two-tailed P=0.018). This suggested that forbs was the preferred spring food, and that cottongrass inflorescenses, although important, was less-preferred.

Spring foods were relatively uncommon on the study area. Forbs had an average coverage of 1.4±0.2% and were recorded in only 15% of the vegetation plots. Cottongrass had an average coverage of 2.6±0.4% and was recorded in only 14% of the plots. These foods were distributed independently, however, as <1% of the plots contained both. The distribution of both forbs and cottongrass differed from a Poisson distribution (one-group χ^2=954, df=1, P<0.0001, and one-group χ^2=5116, df=1, P<000.1, respectively). The variance:mean ratios were 19.5 for forbs and 34.2 for cottongrass, indicating a clumped distribution for both food groups.

As predicted by the food hypothesis, size of female territories in spring was negatively correlated with food density, expressed as the combined coverage of forbs and cottongrass (r_s= -0.717, df=5, P=0.02, Fig. III-2). Also as predicted, territory size was negatively correlated with spring population density (r_s=

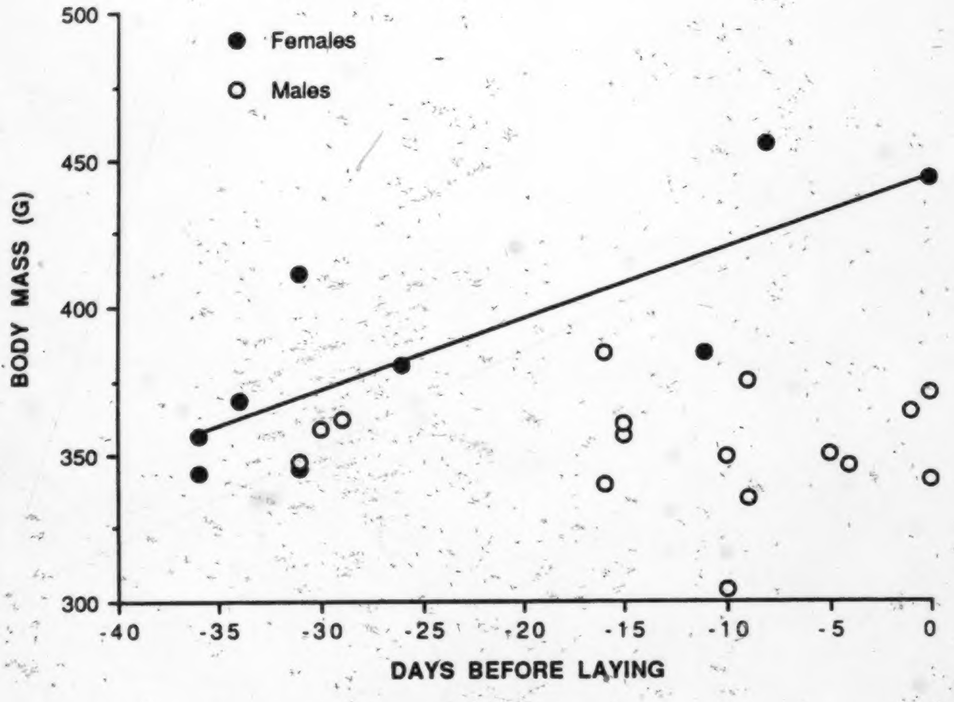

Fig. III-1. Body mass of female and male hazel grouse in relative to the onset of laying in late spring (females: r^2=0.66, df=7, P=0.008, indicated by regression line; males r^2=0.005, df=14, P=0.79).

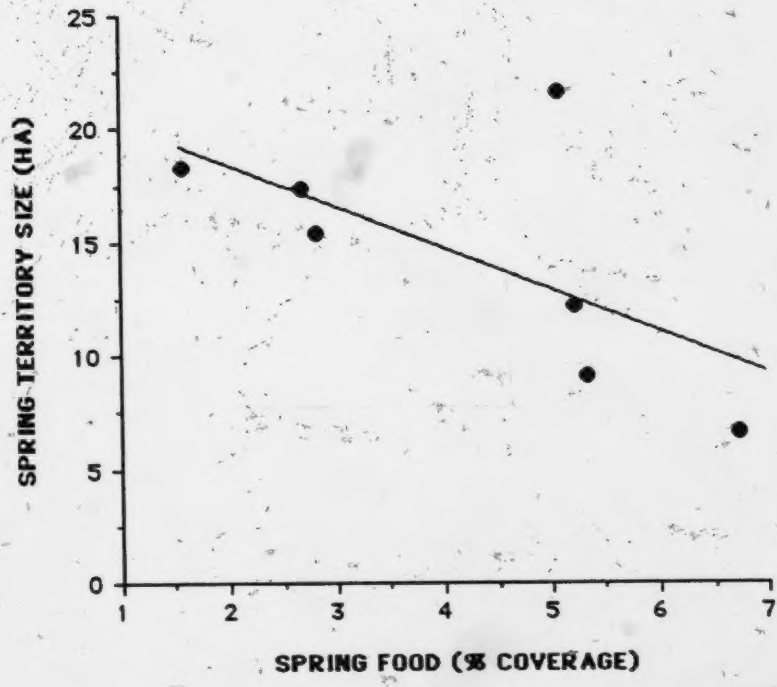

Fig. III-2. Relationship between size of female hazel grouse territories and the density of spring food (forbs and cottongrass combined, r_s= -0.717, df=5, P=0.02).

-0.777, df=5, P=0.03). In contrast, the sizes of male territories were not significantly related to food density (r_s= -0.290, df=12, P=0.15), but they were correlated negatively with spring population density (r_s= -0.482, df=12, P=0.04). For males, the sample size was large enough to subject the data to a stepwise multiple regression, with the same result. Only population density entered as a significant variable (F=5.27, df=1,11, P=0.02); food density was unimportant (F=0.34, df=1,11, P>0.10).

Contrary to the prediction, no relationship was found between the density of spring food on the female territories and clutch size of first clutches (r_s=0.053, df=7, P=0.44) nor between the amount of spring food (density of food times size of territory) and clutch size (r_s=0.264, df=7, P=0.23). However, egg size (mass) and clutch size were positively correlated, both in southern Sweden (r_s=0.792, df=8, P=0.01, Fig. III-3) and Hokkaido, Japan (r_s=0.674, df=10, P=0.01, Fig. III-4). Mass of fresh eggs was calculated using the following formula: mass= -15.08 + 4.98 · (length, cm) + 1.58 · (diameter, cm)^2, which was based on the mass of 29 fresh eggs from four first clutches from Grimsö in spring 1990 (r^2= 0.923, df=27, two-tailed P<0.0001). When first clutches were removed within three days of the start of incubation in 1990, females that laid clutches of six eggs seemed to take longer to renest (17 and 36 days) than those that laid clutches of eight and nine eggs (12 and 11 days, respectively, U=4, df=3, P=0.06). The female that laid eight eggs in her first clutch, laid eight eggs in her second clutch in 11 days. At a laying rate of 1.3 days per egg, she began laying her second clutch about 1.5 days after losing her first clutch. The second clutch of the female that laid nine eggs in her first clutch was taken by a predator before I could count the eggs.

Age of the female did not appear to be an important factor in the variation of clutch size, as the number of eggs in first clutches of adult and yearling females did not differ significantly (t=0.48, df=9, two-tailed P=0.65, Table III-1). However, second clutches contained fewer eggs than first clutches (t=2.35, df=13, two-tailed P=0.04, Table III-1).

The mean mass of 29 fresh eggs from first clutches was 16.8±0.23 g. Thus, the mass of an average clutch (7.6 eggs) was 127.7 g. This was 36% of a female's calculated body mass 36 days before laying and 29% of it at laying. The mass of a fresh clutch of nine eggs, the largest clutch recorded during this study, was 158 g, 44% of a female's body mass 36 days before laying and 36% of it at laying.

The onset of laying, calculated individually for each female and based on the beginning of incubation and clutch size, averaged 7 May 1988 (three nests), 4 May 1989 (two nests) and 26 April 1990 (four nests). This variation was consistent with that of plant phenology on the area; first cottongrass inflorescenses were observed on 25 April 1988, 4 April 1989, and 21 March 1990, and leaf buds of birch (Betula spp.) began opening on 9 May 1988, 14 April 1989, and 5 April 1990.

The nest dispersion hypothesis. The location of 13 nests was

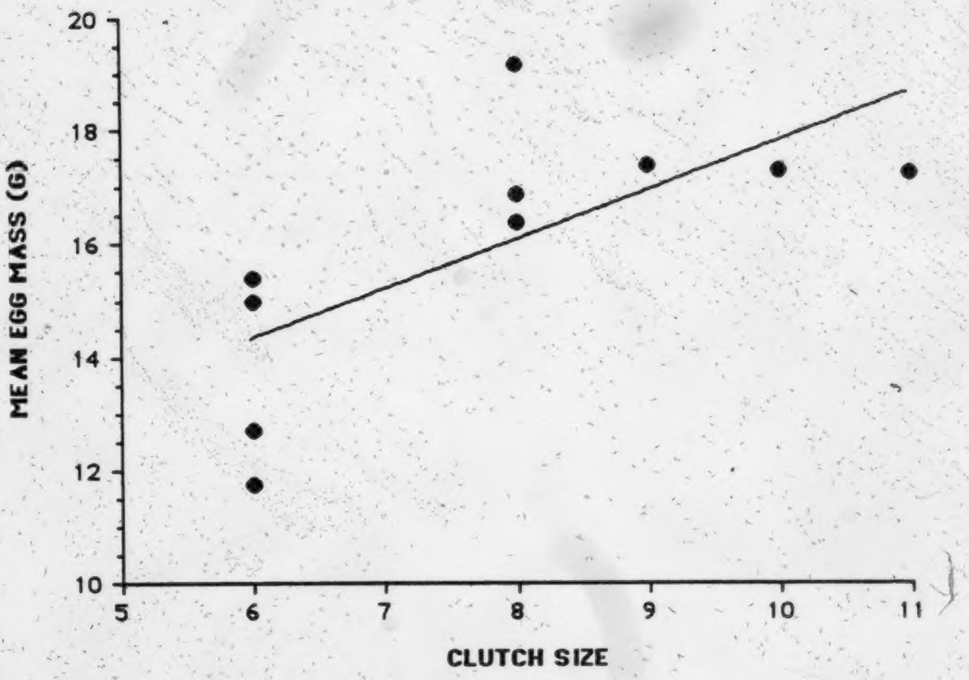

Fig. III-3. Relationship between hazel grouse egg mass and clutch size on and near the study area in southcentral Sweden (r_s=0.792, df=8, P=0.009).

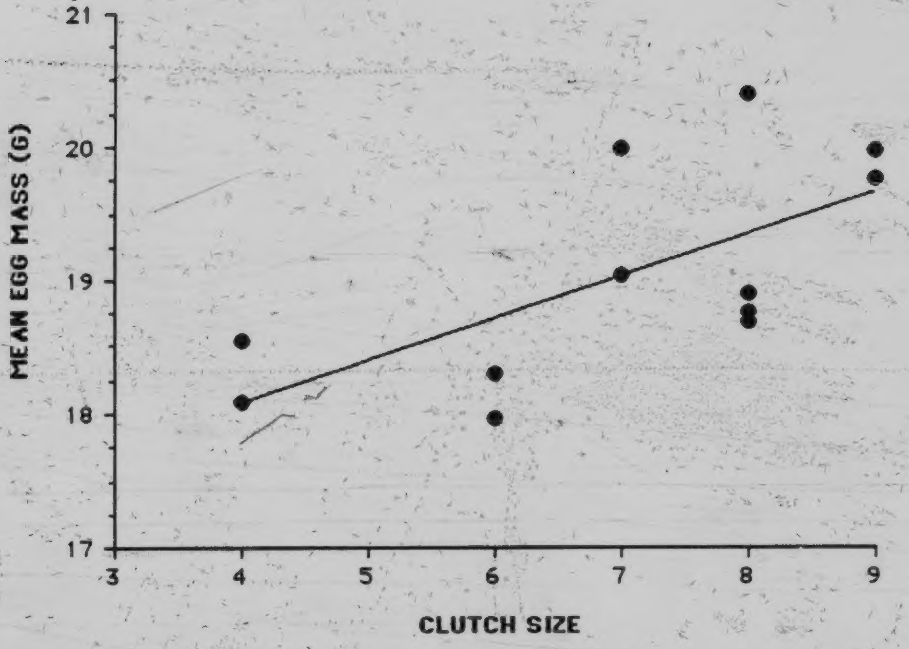

Fig. III-4. Relationship between hazel grouse egg mass and clutch size on Hokkaido Island, Japan (from Haga & Takamata 1986, r_s=0.674, df=10, P=0.012).

Table III-1. Clutch sizes of hazel grouse on the Grimsö Wildlife Research Area, 1988-1990.

Age of female	Type of clutch	Number of eggs						Mean	SE	N
		3	5	6	7	8	9			
Adult	First	0	0	1	1	1	2	7.8	0.6	5
Yearling	First	0	0	2	0	2	1	7.4	0.6	5
Both	First	0	0	3	1	3	3	7.6	0.4	10
Adult	Renest	0	1	0	0	1	0	6.5	1.5	2
Yearling	Renest	1	0	1	0	0	0	4.5	1.5	2
Both	Renest	1	1	1	0	1	0	5.5	1.0	4

plotted within the spring territories of the females. Of these, 42% were located within the inner 50% of the territory (5.5 nests; one was located on the border between the inner and outer 50%). This distribution was not different from that expected from a random distribution of nests (one group χ^2=0.31, df=1, P=0.57).

The nest guarding hypothesis. The data also were not consistent with the nest-guarding hypothesis. Five females were followed during the 10 days prior to the beginning of laying and the laying period. Although these females were located closer to the nest sites during the laying period (240±30 m) than during the prelaying period (274±49), as predicted, the difference was not statistically significant (paired t test, t=1.145, df=4, P=0.16).

Factors promoting monogamous mating

The male sentry hypothesis. The data supported the male sentry hypothesis. The limited data on mortality during late winter and the breeding season suggested that the breeding season, particularly the active and weight gain periods, was more dangerous for females than for males (Table III-2). During these two periods, which lasted 81 days, radio-marked females had a 45% survival rate (N=10 female seasons; 409 radio days), compared to 92% for males (N=16 male seasons; 1029 radio days). This difference was not statistically significant, but tended towards significance (Fisher's exact test, df=1, P<0.10). As predicted, the intrapair distance decreased from late winter to the female active period, and again between the female active period and the prefertile weight gain period (Fig. III-5). Tests of individual pairs revealed one significant decrease in distance for four pairs between the first and second periods, and two significant decreases of three pairs between the second and third periods (Mann-Whitney U tests, P<0.05). All three pairs followed throughout these three periods showed a significant decrease in intrapair distance. Combining all data showed a marginally significant decrease in intrapair distance from the winter to the female active period (U=2047, df=118, P=0.06) and a highly significant decrease from the active period to the prefertile female weight gain period (U=1648.5, df=101, P<0.0001).

The median intrapair distance was correlated positively with the annual survival of hazel grouse on the territory (a measure of security, Chapter VIII) during both the prelaying period (r_s=0.7897, df=5, P=0.03), the renesting period (r_s=0.635, df=7, P=0.04), and both periods combined (r_s=0.722, df=14, P=0.0003, Fig. III-6). The spatial occurrence of potential polyandry among females on the study area also supported the male sentry hypothesis. Overall, 37% of the females were documented to have the opportunity to be polyandrous during 19 receptive periods (Chapter II). The spatial distribution of potential polyandry was related to the annual survival rate on the territory. In the safest territories (no deaths recorded), females were potentially polyandrous in 5 of 8 receptive periods, compared to 2 of 4 in the intermediate territories (42-47% annual survival rates) and 0 of 7 in the most dangerous territories (8-19% survival rates). There was a significantly greater potential for polyandry in the safe and intermediate territories (58%, N=12) than in the most dangerous

Table III-2. Survival rates of radio-marked female and male hazel grouse during the late winter and spring, 1988-1990.

		Period (length in days)			
Sex	Category	Late winter (31)	Active (53)[a]	Weight gain (28)	Fertile (18)
Female	No. birds	5	6	9	8
	No. killed	0	1	3	0
	Bird days	155	279	130	126
	Daily survival	1.0	0.9964	0.9769	1.0
	Survival (%)[b]	100	83	52	100
Male	No. birds	14	13	15	16
	No. killed	1	1	0	0
	Bird days	428	668	361	283
	Daily survival	0.9977	0.9985	1.0	1.0
	Survival (%)[b]	93	92	100	100

[a] Mean for the three years.

[b] Probability to survive the period (daily survival rate raised to the power of the number of days in the period).

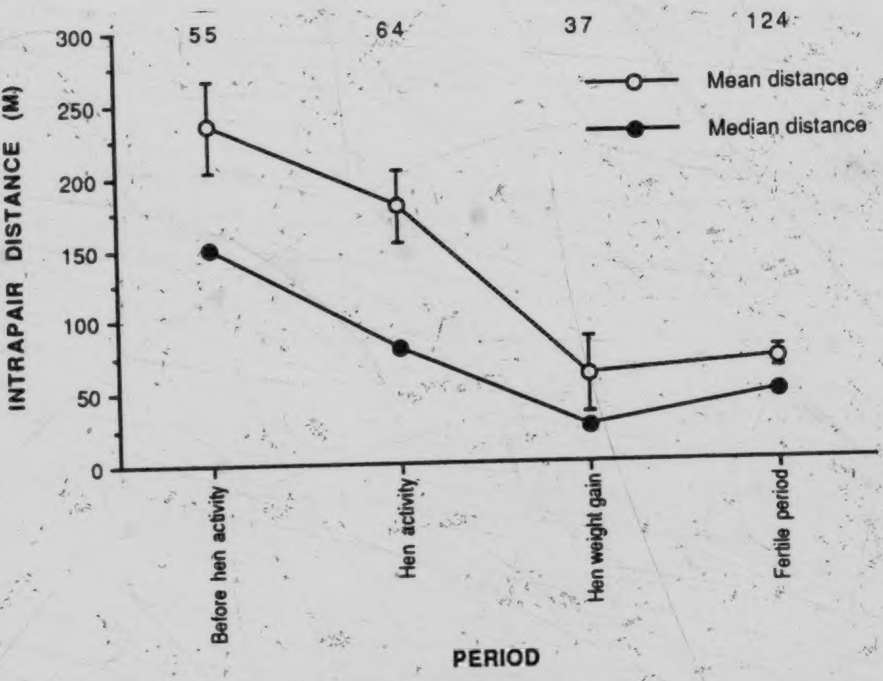

Fig. III-5. Variations in intrapair distance (simultaneously obtained locations between the male and female of a pair of hazel grouse, all pairs combined) during the prebreeding and breeding seasons on the study area. The error bars are standard errors of the mean, and the numbers are sample size.

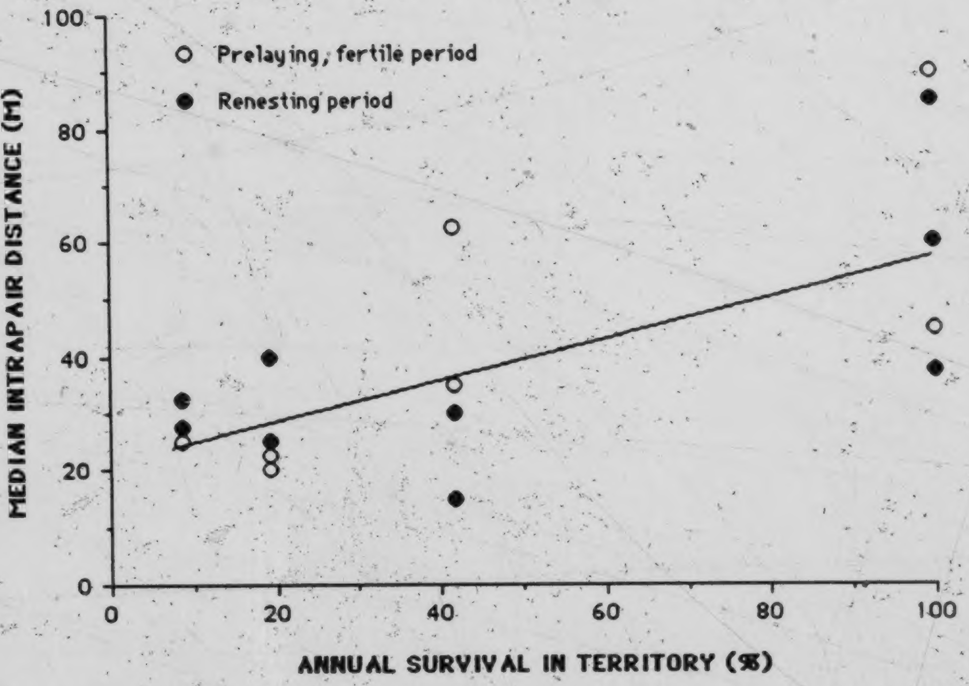

Fig. III-6. Relationship between interpair distances of hazel grouse pairs and the security of their territories, as determined by annual survival of radio-marked hazel grouse (see Chapter VIII) during the prelaying fertile period (r_s= 0.789, df=5, P=0.027) and renesting period (r_s=0.635, df=7, P=0.036). The correlation for the combined data was r_s=0.722, df=14, P=0.0003.

territories (0%, N=7, Fisher's exact test, P=0.016). Also, the rate at which male hazel grouse advertised spontaneously during the prelaying period was correlated positively with the annual survival rate in their territory (r_s =0.544, df=13, P=0.04, Fig. III-7).

The mate guarding hypothesis. The mate guarding hypothesis predicted a decrease in interpair distance from the prefertile weight gain period to the fertile period. This was not found among any of the five pairs followed during these two periods (Mann-Whitney U tests, P>0.05). Also, the combined data showed no change between these two periods (U=1077, df=160, P=0.44, Fig III-4).

The demography hypothesis. The operational sex ratio was male biased, 1.4 males per female (Chapter II). Incubation in first nests of radio-marked females began within about a five-day period each year; 14-19 May 1988 (three nests), between 12-13 and 14-19 May 1989 (two nests), and 4-9 May 1990 (four nests). Renestings were less synchronous, depending on the timing of nest depredation; incubation began on 14 June 1989 and 15 May, 22 May (two nests), and 15 June 1990.

DISCUSSION

Factors promoting female territoriality

Female hazel grouse defend prelaying territories (Chapter II) and are aggressive in captivity in spring (Sugimoto 1986). In this respect, they are similar to other smaller grouse, both forest grouse and ptarmigan (Herzog & Boag 1977, 1978, Maxson 1978, Hannon 1983, Bergerud & Butler 1985). But why do these females defend space? Experiments by Hannon (1984) showed that territoriality allowed monogamous female willow ptarmigan to monopolize one male by excluding other females from his territory. It appeared as though female hazel grouse did not choose a male territory, but that the converse was true (Chapter II). Thus, factors other than the male and the resources of its territory must promote female territoriality in hazel grouse.

The results of this study were consistent with the hypothesis that females defended spring food resources during the prelaying period. Females had a significant nutritional demand during spring, when they were more active than males (Chapter II), they increased in mass by 25% in 36 days, becoming heavier than males before laying (Fig. III-1), and they laid a clutch averaging 36% of their body mass (prior to weight gain) over a 10-day period. Also, captive female hazel grouse rested less and spent more time foraging than males during the prelaying and laying periods (Haga & Takamata 1986, Sugimoto 1986). As predicted, territory size was negatively correlated with population density and food density, suggesting that a resource was defended from competitors (Gauthier 1987, Hixon 1987). A direct relationship between food density or abundance and clutch size was not found, although females with less food may have produced as many eggs as those with more food, with the consequence that condition (body mass) was reduced (Pattenden & Boag

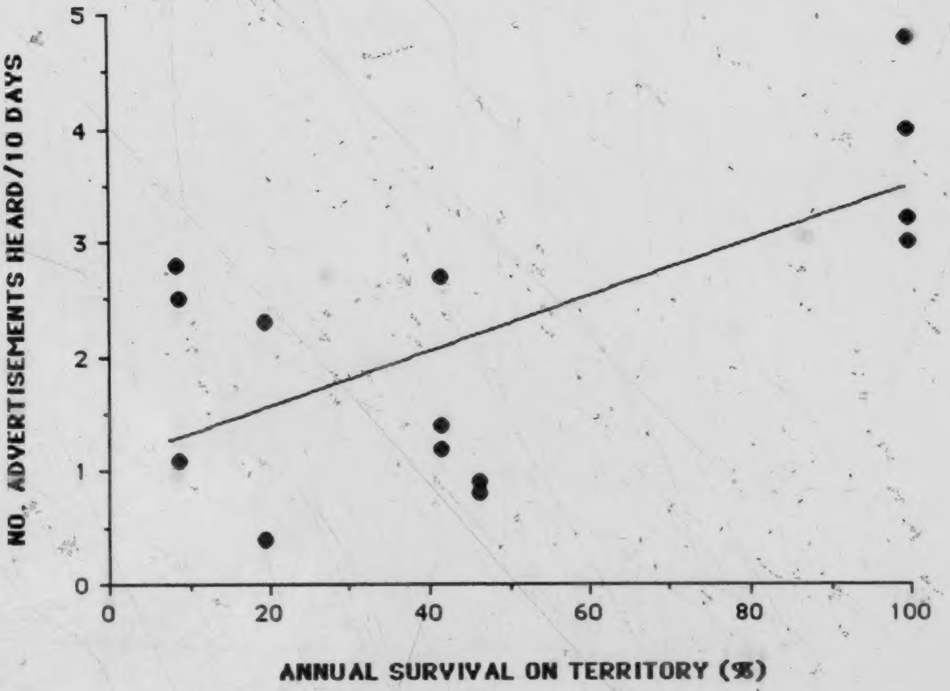

Fig. III-7. The relationship between spontaneous advertisement of male hazel grouse between 1 April and 15 May and the security of their territories, as determined by annual survival of radio-marked hazel grouse (see Chapter VIII); r_s=0.544, df=13, two-tailed P=0.04.

1989, Hannon & Martin in press). However, the indirect predictions were consistent with this hypothesis. Sprouting forbs, which grow in richer soils, were preferred as a spring food. But this food source and the secondary food source, cottongrass inflorescenses, were relatively uncommon on the area and highly clumped in distribution. As predicted by the food hypothesis, sites with richer vegetation were chosen for hazel grouse territories, and spring territories were in richer areas than autumn territories. Also, the size of female territories was negatively correlated with food abundance, whereas the size of male territories was not. In addition, egg size and clutch size were positively correlated both on my study area and on an area in Japan, and females that laid larger first clutches seemed to be able to lay larger second clutches and renest more quickly than females laying smaller first clutches, although this also may have been a consequence of differences is female quality independently of territory quality. Finally, the beginning of laying varied with plant phenology on the area. No female hazel grouse were observed moving into a territory vacated after about 1 April, although they did so before that (Chapter II). On average, the weight gain period began about 27 March during this study, suggesting that females stopped changing territories when acquision of nutrients became a high priority.

Lack (1968) proposed that the clutch size of precocial birds was limited by the ability of the female to produce eggs. This hypothesis appears to be appropriate for grouse because they typically acquire very small energy reserves for the winter (compared to other birds); they survive by feeding regularly and emphasizing energy conservation above energy acquisition (Thomas 1987, 1988). Thus, the importance of exogenous energy and nutrient sources for reproduction has been emphasized in studies of grouse energetics (Thomas et al. 1975, Thomas & Popko 1981, Thomas 1982, Brittas 1984, Remington & Braun 1988, Servello & Kirkpatrick 1988). This has been supported by experiments with captive grouse (Moss et al. 1971, Savory 1975, Sharp & Moss 1981, Beckerton & Middleton 1982) and field studies showing differences in reproduction among areas or years associated with food availability or quality (Siivonen 1957, Moss et al. 1975, Brittas 1988). Captive hazel grouse were found to lay larger clutches than wild grouse, which Sugimoto (1986) attributed to better nutrition among captive birds. Naylor & Bendell (1989) concluded that clutch size might have been limited proximately by food supply in spruce grouse (Dendragapus canadensis), and that spring diet provided about 60% of the protein and 45% of the calcium needed for clutch formation; the rest coming from endogenous reserves. Hazel grouse in my area were probably more dependent upon spring diet for clutch formation than the spruce grouse studied by Naylor & Bendell (1989). In their study, clutch mass was about 22% of female body mass in April; in my study, it was 33%. Thus, a hazel grouse clutch was 50% more costly to produce than a spruce grouse clutch. Also, hazel grouse females were smaller (395 g) than spruce grouse females (adults 549 g, yearlings 510 g). Relative to size, smaller species generally have fewer endogenous reserves than larger species (Peters 1983).

The pattern of nest placement within territories did not support the nest dispersion hypothesis. However, internest spacing was not evaluated directly.

No evidence was found that females were spending more time close to the nests during laying, guarding nests against parasitism by other females, as predicted by the nest guarding hypothesis. Nest parasitism probably does occur, as nests with as many as 19 and 20 eggs have been reported (Pynnönen 1954), which is over twice the mean clutch size (Bergmann et al. 1982, Table III-1). Intraspecific nest paratism has been recorded in willow ptarmigan (Martin 1984) and is common in dense populations of red grouse (S. Redpath, pers. comm.).

I conclude that female defense of prelaying territories secured their access to relatively uncommon and clumped sources of nutritious food that was required at a time when females probably required extra energy and nutrients for egg production. Nest dispersion and nest guarding did not appear to explain the behavior observed in this study, but female territoriality would also cause nests to be dispersed and reduce the chance of nest parasitism. These could be secondary benefits of territoriality.

Factors promoting monogamous mating

All results were consistent with the male sentry hypothesis. During the active and weight gain periods, females were vulnerable to predation (Table III-2), the intrapair distance decreased when the females were most actively foraging and gaining mass, but prior to the fertile period (Fig. III-5), intrapair distances were correlated with security of the territory (Fig. III-6), and monogamy was more common in dangerous territories. The correlation between rate of advertising during the prelaying period and territory security (Fig. III-7) strengthened the conclusion that vulnerability to predation affected breeding behavior.

There was no evidence to support the mate guarding hypothesis. The intrapair distance did not decrease immediately prior to the fertile period (Fig. III-5). In addition, the minimum potential for polyandrous matings among females was 37% and the pairs were only together 37% of the time (Chapter II), which argued against the occurrence of any effective mate guarding, as did the relatively large intrapair distances, especially in the secure territories (Fig. III-6).

The demography hypothesis was supported. The operational sex ratio was male-biased (40% more males than females, Chapter II) and females began incubating within a five-day period each spring. This promotes monogamy because a male with a female can achieve more matings by staying with that female than trying to locate a second female that is not with another male during the short receptive period (Emlen & Oring 1977). However, this hypothesis did not incorporate risk of predation, so did not explain the relationships between mating tactics and territory security mentioned above.

I conclude that male sentry behavior for the female, which probably is stressed for time and nutrients, is the most important factor promoting the pair bond, and therefore monogamous mating, in hazel grouse. The male-biased sex ratio and synchronous breeding appeared to be a secondary, contributing factor that reduced the potential for polygyny, although the male-biased sex ratio may have increased the potential for polyandry. Mate guarding did not appear to be important.

The mating system in hazel grouse

The distribution of limiting resources in the biological or physical environments is recognized as a strong determinant of the nature of individual reproductive patterns (Oring 1982, Beehler 1985). Thus, the fitness costs and benefits of reproductive options may differ among individual males and females and between the sexes, and the mating system is the result of the options taken by individuals of both sexes (Wittenberger 1979). In hazel grouse, the mating system appears to be close to monogamy but potentially tending towards polyandry (Chapter II).

The most important priority for females in the spring may be to defend a territory with a nutritious food supply for the production of eggs. In the autumn-winter period, another uncommon and clumped winter food source also was defended against other females (Chapters IV & VII). Females may defend as rich a territory as possible so as to be able to lay as large a clutch as possible and to renest quickly and lay a relatively large second clutch.

Male and female territories did not coincide during the nonbreeding season (Chapter V), but did during the breeding season (Chapter II). It appeared as though males adjusted their territories to the female territory, not the converse (Chapter II). Unpaired males often left their territories and moved to females, females did not change territories after they began to gain body mass, territories of unpaired males were twice as large as those of paired males, but those of paired males were the same size as those of females, and male territory size did not vary with spring food density, as did those of females. Females foraged intensively during the period before laying (Sugimoto 1986) and suffered relatively high mortality (Table III-2). This high mortality may have been due to being active much of the day (Haga & Takamata 1986, Sugimoto 1986, Fig. II-5), searching intensively for food at the expense of watching for predators, and/or being less willing or able to fly with the large body mass in spring. Females were easier to capture in nets in the prelaying period because they appeared to prefer not to fly. When they did fly, they were noticeably slower and less agile than the males.

The pair bond apparently benefited females because the male probably provided vigilance against predators, particularly in dangerous habitats (Fig. III-6). Hazel grouse have a relatively high mortality rate (Chapter VIII), so females should maximize their efforts to produce a large clutch, as the probability of surviving to the next breeding season is relatively low. Higher feeding rates by females in the prelaying period has been associated with male vigilance in several species of larger birds (Ascroft 1976, Gauthier 1987, Ridley & Hill 1987, Hannon & Martin in press) and in another monogamous galliform, the gray partridge (Perdix perdix), females select more vigilant males in the spring (Dahlgren 1990). In ptarmigan, male vigilance behavior includes behavior to deflect predation from the female to the male (Bergerud 1988), although Gruys (1991) found a higher mortality rate among radio-marked female than male willow ptarmigan during the breeding season and Hannon & Martin (in press) rejected this hypothesis for willow ptarmigan. Bergerud (1988) argued that vigilance of male forest grouse would not be effective, because of the short sighting distances in forest canopies, but stated that, for the hazel grouse, the male may deflect predation from the female at a relatively great mortality price. This argument was apparently not sustained in the case of hazel grouse; mortality appeared to be greater for females than males (Table III-2), suggesting that males did not deflect predation to themselves. It was my impression that the male often warned the female of approaching danger. In more secure habitats, the benefit of this vigilance is apparently less, the intrapair distances greater, and incidence of potentially polyandrous relationships higher.

Males were farther from females in secure habitats (Fig. III-6), which may have reflected a search by the male for females on neighboring territories. This tactic would have been more profitable for a male in a secure territory. The benefit would be an opportunity to mate with two females. Costs would include a lessened likelihood of survival for the "primary" female, but this was offset by the low vulnerability to predation within the territory, and a greater probability that she would mate with another male, which may have occurred often. Perhaps the higher rate of advertising by males in secure territories (Fig. III-7) was to inform both males and other females of the male's presence. A male in a dangerous territory may have had little choice but to stay close to the female, thereby increasing her likelihood of survival. The costs, in terms of reduced female survival, may have outweighed potential advantages gained by searching for matings with other females. Males without females often either left their territory, possibly in search of females, or enlarged the size of their territories, possibly to contact females (Chapter II). Although this behavior may be dangerous, it was perhaps the best available alternative, given the relatively low probability of living until the next breeding season (Chapter VIII). Hannon & Martin (in press) also concluded that monogamy may be prevalent in willow ptarmigan because of constraints to males of obtaining more than one female.

Besides these behavioral factors, monogamy would also be favored at low population densities, as in 1990. Monogamy should also be expected in patches of habitat that are not large enough to support more than one male and one female. Hazel grouse habitat often occurs in such small patches (Bergmann et al. 1982, Chapter VII).

The mating system of males appeared to be shaped by the dispersion and vigilance needs of the female. Thus, the female appears to be the "controlling sex" shaping the mating system (Wittenberger & Tilson 1980). As male hazel grouse do not provide parental care, the potential for polygamy exists among males (Emlen & Oring 1977). This potential was usually not realized because of female need of male vigilance, aggressive defense of territories by females against other females (Hannon 1983), size of defended territories being the same size for males and females (Hannon 1984), male-biased sex ratio (Emlen & Oring 1977), and synchrony of breeding (Emlen & Oring 1977).

The mating systems of the subfamily Tetraoninae

There have been several attempts to identify the factors contributing to the evolution of mating systems in grouse. Vos (1979) concluded that mating system and habitat were related in grouse; tundra species are monogamous and territorial, steppe and forest-edge species lek on arenas, and forest grouse are polygynous and territorial. The hazel grouse and capercaillie (Tetrao urogallus) were awkward exceptions to this generalization.

Wittenberger (1978), in an attempted comparison of food abundance among habitats, concluded that competition for food resources should favor monogamy over polygyny, and that females should forage on male territories to avoid competition with other females and benefit from male vigilance against predators. My study of hazel grouse showed that it was not necessary for females to forage on male territories; females had their own territories.

I propose that it is more realistic to compare grouse in relation to nutritional needs of the female during the prelaying period, which is related to female body size. Energy stress is greatest among small females, because they lay a relatively greater mass of eggs than those of larger species (Sæther & Andersen 1988), require relatively more nutritious foods, and have relatively smaller endogenous reserves, corrected for body size (Peters 1983). Therefore, food resources should be more important for territory selection by smaller females and they should be expected to devote greater amounts of time to foraging in spring to produce a clutch, likely exposing themselves to a greater risk of predation. Male sentry behavior should be important to small females because of this high predation risk. This predicts that territoriality should be stronger in small species and that mortality of females should be relatively higher than males in the species with energetically relatively more costly reproduction.

Comparisons among species support these predictions. The social organization of females prior to mating varied by female size. Of 17 species, those with pair bonds were smallest (mean rank of female size was 3.8), those dispersed solitarily were intermediate (mean rank of 7.5), and those that stayed in groups until mating were largest (mean rank of 13, Kruskall-Wallis H=10.7, df=2, two-tailed $P<0.005$). This relationship is more evident when the species are divided into those in open habitats and those in forests, which suggests that habitat was also important (Fig. III-8). Also, the degree of territoriality diminishes with increasing size of female grouse (Table III-3), which may be a general phenomenon, because in herbivorous mammals, the home range also is shared with an increasing number of conspecifics with increasing body size (Damuth 1981). Spring food may be an important component of female hazel grouse (this study) and spruce grouse territories (Naylor & Bendell 1989). In the willow ptarmigan, food appears to be more important in some places (Moss 1972) than others (Steen et al. 1985); in the red grouse, it appears to be an important component of the territory (Moss et al. 1988). Endogenous reserves provide only half the lipids required for egg production in willow ptarmigan (Brittas 1984). Schieck (1988) found that factors associated with the territory accounted for 80% of the variation in clutch size in a willow ptarmigan

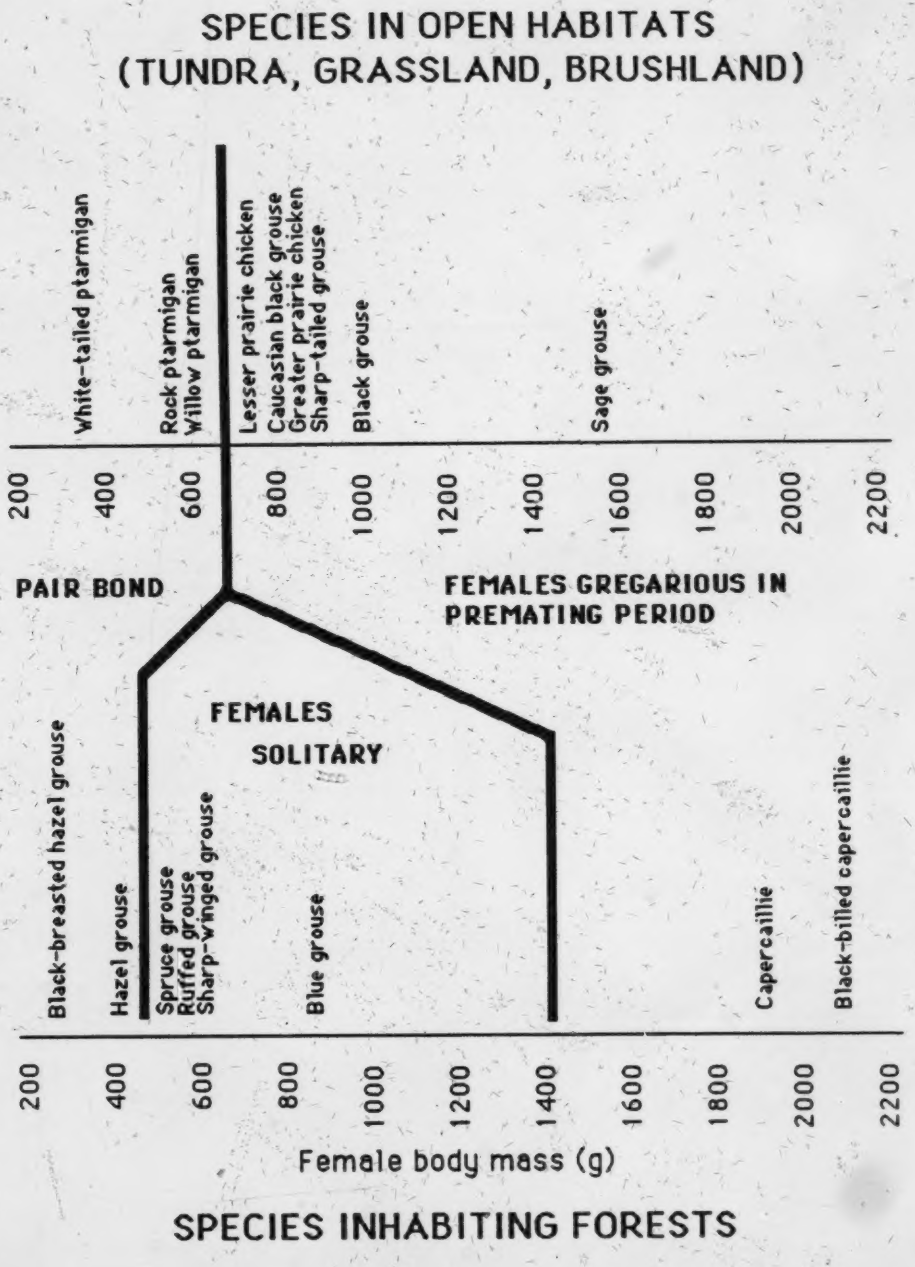

Fig. III-8. Relationship between the body mass of female grouse and their social behavior during the premating period in open and forested habitats (based on reviews in Hjorth 1970, Johnsgard 1983, Klaus et al. 1989, 1990).

Table III-3. Degree of female territoriality among grouse during the prelaying period, measured as overlap of neighboring territories, in relation to the body mass of females and type of habitat.

	Female body	Overlap (%) & habitat					
		Open habitats		Forests			
Species	mass[a]	<5	>20	<5	5-20	>20	Source
Capercaillie	1880					X	Wegge 1984
Sage grouse	1554		X				Gibson & Bradbury 1986
Black grouse	913		X				Willebrand 1988
Blue grouse	840				X		Hines 1986
Sharp-tailed grouse	815		X				Gratson 1988
Prairie chicken	770		X				Svedarsky 1988
Willow pt.	588	X					Hannon 1983
Rock pt.	564	X					R. Cotter, p. c.[b]
Ruffed grouse	543				X		Maxson 1978
Spruce grouse	538				X		Herzog & Boag 1978
Hazel grouse	396			X			This study

[a] In grams, from Johnsgard (1983).

[b] Personal communication.

population. The largest grouse, the capercaillie, is not particularly stressed for energy during the breeding period (Lindén 1984). Female capercaillie space themselves in a manner suggesting territoriality during the late prelaying period (Wegge 1984), but other factors, such as protecting nest sites from intraspecific nest parasitism or nest dispersion as a predator avoidance mechanism, may be more important than defense of food.

Female willow ptarmigan are alert less and forage more when accompanied by the male, and they appear to benefit from male vigilance and parental care, at least during some years (Miller & Watson 1978, Hannon 1984, Hannon & Martin in press). Moreover, among grouse species, a correlation exists between adult sex ratio and degree of sexual dimorphism (Wittenberger 1978), which is itself correlated with female body mass (Wiley 1974) and suggests that smaller females suffer relatively higher mortality, compared to males of the same species, than larger females. However, this relationship is biased somewhat because sex ratios of the largest and most sexually dimorphic species are also affected by higher mortality of juvenile males than females during their first summer of life (Wegge 1980, Lindén 1981, Swenson 1986). Ptarmigan females are more nutritionally stressed during the breeding season than other grouse of their size, because they are also molting, which is energetically expensive (Lindén 1984, Gardarsson & Moss 1970).

According to my model, nutritional stress declines with increasing size of females, and forest grouse females larger than hazel grouse apparently do not benefit from male protection. All larger females in open habitats presumably need vigilance protection from predators, and as they are not territorial to defend food, they form flocks and forage together prior to the mating period (Fig. III-8); the two largest species in forests inhabit open forests (Klaus et al. 1989). Female ring-necked pheasants (Phasianus colchicus), about the size of black grouse, also forage together during the prelaying period, and spend less time alert and more time foraging when in a group than when alone (Ridley & Hill 1987). Flocks of female grouse break up abruptly at the time of mating, and the females are then dispersed (Angelstam et al. 1985, Gratson 1988, Hartzler & Jenni 1988). Presumably a factor besides food is the reason for this dispersion.

The dispersion pattern shown by male grouse during the mating season is probably dictated by that of females (Bradbury 1981). Thus, an important question in understanding the evolution of lekking behavior is: what promotes the evolution of tolerance among females (Schroeder 1990)? My model suggests that monogamous or near-monogamous systems occur where small females, stressed for nutrients, defend territories and require male vigilance. Males have dispersed territories where larger females that are less nutritionally stressed still defend territories, but do not require male vigilance. This apparently only occurs in forested habitats, where more cover is available. Lekking behavior occurs where medium-sized and larger females occur in open habitats. Females do not defend territories prior to mating and depend on flocking with other females as a defense against predators. Males occur in a clumped manner because females are clumped at the time of mating.

My model is female-based and suggests that the effects of ecological factors on mating tactics of individuals should differ for large and small females, and should be viewed along a continuum. Other models relating body size to mating systems in grouse have been male-based. Wiley (1974) proposed that large body size of males was related to increased sexual dimorphism, which led to sexual bimaturism and promiscuity. Sæther & Andersen (1987) proposed that large grouse species were polygynous because larger males have higher survival rates and males with high survival rates should be polygynous to maximize fitness

Hannon's (1984) conclusion that monogamy in willow ptarmigan was promoted by female territoriality, which impeded other females from settling in a male's territory and allowed a female exclusive access to a vigilant male is consistent with my model. However, Oring's (1982) conclusion that ruffed grouse males displayed a male-dominance polygyny because females utilized areas too large for a male to defend was not consistent with my model. I believe this was an unreasonable conclusion, because female ruffed grouse have home ranges of about 12 ha (review in Oring 1982), which is smaller than male hazel grouse territories in spring (17 ha, Chapter II). Ruffed grouse are about 50% larger than hazel grouse (Johnsgard 1983), so a male ruffed grouse should be able to defend 12 ha.

In my model, the hazel grouse is not an exception, as it was in the model of Vos (1979). Also, the hazel grouse did not fit in the models of Wittenberger (1978) and Bergerud (1988), who stressed the value of male vigilance in open habitats, and have stated that two birds together should be more vulnerable to predation than one in dense habitats. Also, the capercaillie was an exception in Vos' (1979) model because it is a forest grouse but has a dispersion system with similarities to both the dispersed territoriality characteristic of forest grouse and the lekking behavior characteristic of grouse in open habitats (Wegge & Larsen 1987). Therefore, the mating system of capercaillie was classified as having dispersed territories by Wittenberger (1978), as lekking by Wiley (1974), and as intermediate by Vos (1979) and Oring (1982). According to my model, the intermediate dispersion pattern of male capercaillie is due to the intermediate dispersion pattern of females. They are large, and therefore do not defend feeding territories, but both species inhabit open forests, and they form smaller flocks during premating than the species in more open habitats (Klaus et al. 1989). Thus, the dispersion pattern of capercaillie females is intermediate between that of solitary females (and dispersed males) and gregarious females (and lekking males).

Was the ancestral grouse monogamous?

The hazel grouse has many primitive characteristics, including morphology, behavior, and inhabiting forested habitats (Short 1967, Hjorth 1970, Vos 1979, Scherzinger 1981). This has led some to conclude that the basic grouse mating system was monogamy (Short 1967, Hjorth 1970, Johnsgard 1983). I argue that the mating system of hazel grouse is related to its small size. According to the model of mating systems presented here, the first question to answer is how large was the ancestral grouse. If it was medium-sized, which seems reasonable, it is unlikely that the ancestral grouse had a mating system similar to that of hazel grouse. Furthermore, hazel grouse in secure territories probably often did not mate monogamously and the pair bond was relatively weak. The mating system of a medium-sized ancestral grouse probably consisted of dispersed territorial males and females, such as is found in North American forest grouse. Short (1967) considered the spruce grouse and the black-breasted hazel grouse (*Bonasa sewerzowi*) to be closest morphologically to the ancestral form. As the black-breasted hazel grouse is the smallest grouse, the spruce grouse may serve as a better model of the basic grouse mating system.

LITERATURE CITED

Ahnlund, H. & B. Helander. 1975. The food of hazel grouse (*Tetrastes bonasia* L.) in Sweden. Viltrevy 9:221-240.

Angelstam, P. K., M. Jaarola & N.-E. Nordh. 1985. Are female black grouse *Tetrao tetrix* territorial? Ornis Fennica 62:124-129.

Ashcroft, R. E. 1976. A function of the pairbond in the common eider. Wildfowl 27:101-105.

Beckerton, P. R. & A. L. A. Middleton. 1982. Effects of dietary protein levels on ruffed grouse reproduction. J. Wildl. Manage. 46:569-579.

Beehler, B. 1985. Adaptive significance of monogamy in the trumpet manucode *Manucodia keraudrenii* (Aves: Paradisaeidae). Ornithol. Monogr. 37:83-99.

Bergerud, A. T. 1988. Mating systems in grouse. Pp. 439-472 *in* A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Bergerud, A. T. & H. E. Butler. 1985. Aggressive and spacing behavior of female blue grouse. Auk 102:313-322.

Bergerud, A. T. & M. W. Gratson. 1988. Survival and breeding strategies of grouse. Pp. 473-577 *in* A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Bergerud, A. T. & D. H. Mossop. 1984. The pair bond in ptarmigan. Can. J. Zool. 62:2129-2141.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn *Bonasa bonasia*, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Björklund, M. & B. Westman. 1986. Mate-guarding in the great tit: tactics of a territorial forest-living species. Ornis Scand. 17:99-105.

Bradbury, J. W. 1981. The evolution of leks. Pp. 138-169 in R. D. Alexander & D. W. Tinkle. Natural selection and social behaviour. Chiron, New York.

Brittas, R. 1984. Seasonal and annual changes in condition of the Swedish willow grouse, Lagopus lagopus. Finnish Game Res. 42:5-17.

Brittas, R. 1988. Nutrition and reproduction of the willow grouse Lagopus lagopus in central Sweden. Ornis Scand. 19:49-57.

Brodsky, L. M. 1988. Mating tactics of male rock ptarmigan, Lagopus mutus: a conditional mating strategy. Anim. Behav. 36:335-342.

Comeau, R. M. & D. M. Keppie. 1989. Crop weights used to adjust body weights of live spruce grouse. J. Wildl. Manage. 53:818-819.

Dahlgren, J. 1990. Females choose vigilant males: an experiment with the monogamous grey partridge, Perdix perdix. Anim. Behav. 39:646-651.

Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. Biol. J. Linnean Soc. 15:185-193.

Dunn, P. O. & S. J. Hannon. 1989. Evidence for obligate male parental care in black-billed magpies. Auk 106:635-644.

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Gardarsson, A. & R. Moss. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. Pp. 47-69 in A. Watson, ed. Animal populations in relation to their food resources. Blackwell Sci. Publ., Oxford.

Gauthier, G. 1987. The adaptive significance of territorial behaviour in breeding buffleheads: a test of three hypotheses. Anim. Behav. 35:348-360.

Gibson, R. M. & J. W. Bradbury. 1986. Male and female mating strategies on sage grouse leks. Pp. 379-398 in R. I. Rubenstein & R. W. Wrangham, eds. Ecological aspects of social evolution, birds and mammals. Princeton Univ. Press, Princeton, New Jersey.

Gowaty, P. A., J. H. Plissner & T. G. Williams. 1989. Behavioural correlates of uncertain parentage: mate guarding and nest guarding by eastern bluebirds, Sialia sialis. Anim. Behav. 38:272-284.

Gratson, M. W. 1988. Spatial patterns, movements, and cover selection by sharp-tailed grouse. Pp. 158-192 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Gruys, R. C. 1991. Autumn and winter movements and mortality of willow ptarmigan at Chilkat Pass, B.C. M. S. thesis, Univ. Alberta, Edmonton.

Haga, R. & S. Takamata. 1986. Ecology and breeding biology of the hazel grouse Tetrastes bonasia in captivity. 1. Breeding, artificial insemination (sic. incubation), and rearing control. Tori 34:105-125. (In Japanese, English summ.)

Hägglund, B. & J.-E. Lundmark. 1984. Handledning i bonitering med Skogshögskolans boniteringssystem. Del 3, Markvegetationstyper -- Skogsmarksflora. Skogsstyrelsen, Jönköping. (In Swedish)

Hannon, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alteration of sex ratio. J. Anim. Ecol. 52:807-820.

Hannon, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Anim. Behav. 32:153-161.

Hannon, S. J. & K. Martin. In press. Monogamy in willow ptarmigan: is male vigilance necessary for reproductive success and survival of females? Anim. Behav.

Hartzler, J. E. & D. A. Jenni. 1988. Mate choice by female sage grouse. Pp. 240-269 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Harvey, M. J. & R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum home range method. J. Mammal. 46:398-402.

Herzog, P. W. & D. A. Boag. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Can. J. Zool. 55:1734-1739.

Herzog, P. W. & D. A. Boag. 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. 42:853-865.

Hines, J. E. 1986. Recruitment of young in a declining population of blue grouse. Ph. D. thesis. Univ. Alberta, Edmonton.

Hixon, M. A. 1987. Territory area as a determinant of mating systems. Am. Zool. 27:229-247.

Hjorth, I. 1979. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7:183-596.

Högstedt, G. 1981. Effect of additonal food on reproductive success in the magpie (Pica pica). J. Anim. Ecol. 50:219-229.

Johnsgard, P. A. 1983. The grouse of the world. Univ. Nebraska Press, Lincoln.

Kenward, R. 1987. Wildlife radio tagging; equipment, field techniques and data analysis. Academic Press, London.

Klaus, S., A. V. Andreev, H.-H. Bergmann, F. Müller, J. Porkert & J. Wiesner. 1989. Die Auerhühner, Tetrao urogallus und T. urogalloides. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Klaus, S., H.-H. Bergmann, C. Marti, F. Müller, O. A. Vitovich & J. Wiesner. 1990. Die Birkhühner, Tetrao tetrix und T. mlokosiewiczi. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Kleiman, D. G. 1977. Monogamy in mammals. Quart. Rev. Biol. 52:39-69.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London.

Lindén, H. 1981. Estimation of juvenile mortality in the capercaillie, Tetrao urogallus, and the black grouse, Tetrao tetrix, from indirect evidence. Finnish Game Res. 39:33-51.

Lindén, H. 1984. Annual patterns in the ecological energetics of the capercaillie, Tetrao urogallus, in captivity. Finnish Game Res. 42:19-27.

MacLean, S. F. & T. R. Seastedt. 1979. Avian territoriality: sufficient resources or interference competition? Am. Nat. 114:308-312.

Martin, K. 1984. Intraspecific nest parasitism in willow ptarmigan. J. Field Ornithol. 55:250-251.

Martin, K. & F. Cooke. 1987. Bi-parental care in willow ptarmigan: a luxury? Anim. Behav. 35:369-379.

Maxson, S. J. 1977. Activity patterns of female ruffed grouse during the breeding season. Wilson Bull. 89:439-455.

Maxson, S. J. 1978. Spring home range and habitat use by female ruffed grouse. J. Wildl. Manage. 42:61-71.

Miller G. R. & A. Watson. 1978. Territories and the food plant of individual red grouse. I. Territory size, number of mates, and brood size compared with the abundance, production and diversity of heather. J. Anim. Ecol. 47:293-305.

Mock, D. W. 1985. An introduction to the neglected mating system. Ornithol. Monogr. 37:1-10.

Moss, R. 1972. Social organization of willow ptarmigan on their breeding grounds in interior Alaska. Condor 74:144-151.

Moss, R., A. Watson, R. Parr & W. Glennie. 1971. Effects of dietary supplements of newly growing heather on the breeding of captive red grouse. Br. J. Nutr. 25:135-143.

Moss, R., A. Watson & R. Parr. 1975. Maternal nutrition and breeding success in red grouse (Lagopus lagopus scoticus). J. Anim. Ecol. 44:233-244.

Moss, R., A. Watson & R. Parr. 1988. Mate choice by hen red grouse Lagopus lagopus with an excess of cocks--role of territory size and food quality. Ibis 130:545-552.

Naylor, B. J. & J. F. Bendell. 1989. Clutch size and egg size of spruce grouse in relation to spring diet, food supply, and endogenous reserves. Can. J. Zool. 67:969-980.

Nugent, D. P. & D. A. Boag. 1982. Communication among territorial female spruce grouse. Can. J. Zool. 60:2624-2632.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.

Oring, L. W. 1982. Avian mating systems. Avian Biol. 6:1-92.

Pattenden, R. K. & D. A. Boag. 1989. Effects of body mass on courtship, pairing and reproduction in captive mallards. Can. J. Zool. 67:495-501.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Remington, T. E. & C. E. Braun. 1988. Carcass composition and energy reserves of sage grouse during winter. Condor 90:15-19.

Ridley, M. W. & D. A. Hill. 1987. Social organization in the pheasant (Phasianus colchicus): harem formation, mate selection and the role of mate guarding. J. Zool., London 211:619-630.

Sæther, B.-E. & R. Andersen. 1988. Ecological consequences of body size in grouse Tetraonidae. Fauna norv. Ser. C, Cinclus 11:19-26.

Savard, J.-P. L. 1988. Winter, spring and summer territoriality in Barrow's goldeneye: characteristics and benefits. Ornis Scand. 19:119-128.

Savory, C. J. 1975. Seasonal variations in the food intake of captive red grouse. Br. Poult. Sci. 18:471-479.

Scherzinger, W. 1981. Stimminventar und Fortpflanzungsverhalten des Haselhuhnes Bonasa bonasia. Ornithol. Beob. 78:57-86.

Schieck, J. 1988. Territory selection and site fidelity in willow ptarmigan: the importance of quality and familiarity with territory and partner. Ph. D. thesis, Univ. Alberta, Edmonton.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Schroeder, M. A. 1990. Movement and dispersion of greater prairie-chickens in northeastern Colorado. Ph. D. thesis, Colorado State Univ., Fort Collins.

Servello, F. A. & R. L. Kirkpatrick. 1988. Nutrition and condition of ruffed grouse during the breeding season in southwestern Virginia. Condor 90:836-842.

Sharp, P. J. & R. Moss. 1981. A comparison of the responses of captive willow ptarmigan (Lagopus lagopus lagopus), red grouse (Lagopus lagopus scoticus), and hybrids to increasing daylengths with observations on the modifying effects of nutrition and crowding in red grouse. Gen. Comp. Endocrinol. 45:181-188.

Short, L. L., Jr. 1967. A review of the genera of grouse (Aves, Tetraoninae). Am. Mus. Novitates No. 2289.

Siivonen, L. 1957. The problem of the short-term fluctuations in numbers of tetraonids in Europe. Pap. Game Res. 19:1-44.

Steen, J. E., H. C. Pedersen, K. E. Erikstad, K. B. Hansen, K. Høydal & A. Størdal. 1985. The significance of cock territories in willow ptarmigan. Ornis Scand. 16:277-282.

Stenman, O. & M. Helminen. 1974. Aging method of hazel grouse (Tetrastes bonasia) based on wings. Suomen Riista 25:90-96. (In Finnish, English summ.)

Sugimoto, M. 1986. Captive breeding and behavioral analysis of the hazel grouse Tetrastes bonasia. Thesis, Obihiro Univ. of Agr. and Vet. Med., Obihiro, Japan.

Svedarsky, W. D. 1988. Reproductive ecology of female greater prairie chickens in Minnesota. Pp. 193-239 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Swenson, J. E. 1986. Differential survival by sex in juvenile sage grouse and gray partridge. Ornis Scand. 17:14-17.

Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse Bonasa bonasia in spring and autumn. Ornis Fennica 68:in press.

Thomas, V. G. 1982. Energetic reserves of Hudson Bay willow ptarmigan during winter and spring. Can. J. Zool. 60:1618-1623.

Thomas, V. G. 1987. Similar winter energy strategies of grouse, hares and rabbits in northern biomes. Oikos 50:206-212.

Thomas, V. G. 1988. Body condition, ovarian hierarchies, and their relation to egg formation in anseriform and galliform species. Acta Congr. Intern. Ornithol. 19:353-363.

Thomas, V. G., H. G. Lumsden & D. H. Price. 1975. Aspects of the winter metabolism of ruffed grouse (Bonasa umbellus) with special reference to energy reserves. Can. J. Zool. 53:434-440.

Thomas, V. G. & R. Popko. 1981. Fat and protein reserves of wintering and prebreeding rock ptarmigan from south Hudson Bay. Can. J. Zool. 59:1205-1211.

Trent, T. T. & O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459-472.

Verner, J. & M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143-147.

Vos, G. J. de. 1979. Adaptedness of arena behaviour in black grouse (Tetrao tetrix) and other grouse species (Tetraoninae). Behaviour 68:277-314.

Wegge, P. 1980. Distorted sex ratio among small broods in a declining capercaillie population. Ornis Scand. 11:106-109.

Wegge, P. 1984. Spacing pattern and habitat use of capercaillie hens in spring. Proc. Intern. Symp. on Grouse 3:261-277.

Wegge, P. & B. B. Larsen. 1987. Spacing of adult and subadult male common capercaillie during the breeding season. Auk 104:481-490.

Wiley, R. H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49:201-227.

Willebrand, T. 1988. Demography and ecology of a black grouse (Tetrao tetrix L.) population. Ph. D. thesis, Uppsala Univ., Uppsala, Sweden.

Wittenberger, J. F. 1978. The evolution of mating systems in grouse. Condor 80:126-137.

Wittenberger, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in P. Marler & J. Vandenbergh, eds. Handbook of behavioral neurobiology, Vol. 3. Social behavior and communication. Plenum Press, New York.

Wittenberger, J. F. & R. L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11:197-232.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc. Engelwood Cliffs, New Jersey, USA.

IV. SOCIAL ORGANIZATION OF HAZEL GROUSE DURING THE NONBREEDING PERIOD AND ITS CONSEQUENCES FOR POPULATION REGULATION

INTRODUCTION

There has been much controversy about the role of intrinsic and extrinsic mechanisms in regulating the densities of vertebrates (Lack 1966, Chitty 1967, Brown 1969a, Klomp 1972). Recently, there has been considerable, and often heated, disagreement about the importance of these two mechanisms in limiting population size in grouse (Bergerud & Butler 1985, Bergerud et al. 1985, Bergerud 1987, Hannon & Zwickel 1987, Watson & Moss 1987, 1988, Angelstam 1988, Hannon 1988). Of course, these hypotheses are not mutually exclusive, as populations limited by intrinsic mechanisms at higher densities may be limited by extrinsic factors such as predation or food shortage in certain years (Klomp 1972, Watson & Moss 1979) or in less suitable habitats (Boag & Schroeder 1987).

Recently, Leclerq (1988) proposed that autumn territoriality in hazel grouse (Bonasa bonasia) resulted in the regulation of population size at that time. However, territorial behavior may only serve to space birds within the habitat (Lack 1966, Bergerud & Butler 1985, Bergerud et al. 1985) or to serve as a cue to population density (Klyver & Tinbergen 1953, Fretwell & Lucas 1970), without limiting population size. Fretwell & Lucas (1970) proposed testable hypotheses to determine if territorial behavior resulted in ideal free distribution of birds (settling birds can choose where to settle and all inhabited habitats are equally suitable) or ideal dominance distribution, later renamed ideal despotic distribution (Fretwell 1972) (settling birds are not free to choose and are forced to settle in less suitable habitats when previously settled, more dominant birds already occupy the most suitable habitats). Lindén & Wikman (1983) found that hazel grouse settled in preferred habitats first and secondary habitats after preferred habitats were filled, but they did not speculate about the mechanism, whether it was an ideal free or despotic distribution.

The essential characteristics of a territory are that it is a fixed area, the possessor performs acts of territorial defense, and the area becomes an exclusive area with respect to rivals (Brown & Orians 1970). If territorial behavior in autumn is involved in the regulation of hazel grouse population size at that time, it is important to determine whether winter food is the limiting factor that is defended (Enoksson 1990). If so, territory size should be a result of a balance between the costs and benefits involved, and vary inversely with winter food density (benefit) and intruder pressure (cost of defense) (Brown 1969a, Brown & Orians 1970, Hixon 1980, 1987, Gauthier 1987, Schoener 1987).

Although the territorial behavior of male hazel grouse has been well described (Pynnönen 1954, Ivanter 1962, Klaus et al. 1975, Scherzinger 1981, Bergmann et al. 1982), territorial behavior has not been documented in females. If territoriality is a mechanism regulating population size, then females must also be involved (Hannon 1983). The social organization of hazel grouse is poorly known. The species inhabits dense forests and is difficult to observe

(Bergmann et al. 1982), and no studies have been published on the behavior of hazel grouse based on marked birds. Thus, it has not been documented whether hazel grouse actually defend fixed and exclusive areas at all.

The first objective of this study was to document the social organization of both male and female hazel grouse during the nonbreeding period using radio-marked birds. The second objective was to evaluate Leclerq's (1988) hypothesis that autumn territoriality resulted in the regulation of population size, and, if so, whether winter food was the defended resource. The third objective was to compare the system documented in hazel grouse with that in other species of grouse.

STUDY AREA AND METHODS

The study area (285 ha, 195 ha of forest) was within a forest reserve on the Grismö Wildlife Research Area in southcentral Sweden (59-60° N and 15-16° E). It is described in detail in Chapter VII.

The study encompassed three nonbreeding periods, 1987-88 through 1989-90, and was based on radiotelemetry. Hazel grouse were captured in spring and autumn by luring or chasing them into nylon fishing nets. They received ca. 16-g necklace-type transmitters (Kenward 1987) that weighed ca. 4.5% of the birds' weight. Age was determined by the coloration of the innermost primary (Stenman & Helminen 1974). Here, birds are termed juveniles until they enter their first spring after hatching and yearlings during that spring and the following summer (when they still retain juvenal primaries).

The nonbreeding period was divided into three seasons: summer (June-August), autumn (September-October), and winter (November-March). These were determined *a priori* based on a study of hazel grouse behavior in Finland at a similar latitude (Pynnönen 1954). The size and configuration of territories were determined during each season for birds with 25 or more relocations using the method of Harvey & Barbour (1965). Most of relocations were based on three triangulations, or two if the bird was within 100-150 m. Relocation accuracy was checked in winter, when tracks could be located, and with incubating and dead birds. The determined location was $\leq$20 m of the actual location for 74% of the checks (N=72). Territory size was measured from a 1:15,000 map with a Kempten planimeter. Territory overlap was the mean, in percent, of what the overlap constituted for each territory. Neighbors were radio-marked birds with no known territories between them.

All spontaneous advertisement (vocal and wing-produced) heard in the field was recorded. Total rate of advertisement was the number of instances heard per 10 field days, whereas rate for individual radio-marked birds was the number heard per relocation during September-November. A border dispute was defined arbitrarily as an instance of two or more radio-marked birds of the same sex located within 60 m of each other at a territorial boundary. Unmarked birds also were included when they were heard exchanging territorial advertisement with a radio-marked bird near its boundary. Index of activity was the percentage of the relocations during a month that birds were active, determined by changes in signal strength during triangulation. Rate of movement was the distance between locations of a hazel grouse on consecutive days. All birds of each sex were combined to determine these rates because I was documenting patterns and performing no statistical tests.

The reaction of territorial females to the "hen call" (Hennenruf, a female aggressive call, Scherzinger 1981) in autumn was determined to test if females reacted aggressively towards intruding females. The hen call was imitated using a Wusperl whistle (Bergmann et al. 1982:34). After locating a radio-marked female, I hid 50-150 m from it. I then whistled once per minute for 20 minutes, checking signal strength every five minutes. Afterwards, I relocated her to determine movement, and if she was not with a radio-marked male, I approached her quietly to determine if she was with a male. A female was considered to respond aggressively if it approached or gave a territorial advertisement during the trial period. I used a mounted female to see if the females would attack it only in 1988.

The study area was covered several times a month. The arrival of a new bird following the death of a territory holder was usually detected within one month by seeing it with a radio-marked bird of the opposite sex, hearing or seeing it, obtaining an answer to the hunter's whistle, or finding tracks in the snow. The study area was censused every autumn and spring following the method of Swenson (1991), which is 80-85% effective in locating territorial males. Winter density was the mean of the censuses in autumn and the following spring. The time it took a responding male to announce its presence or be seen following the beginning of whistling at a census stop was recorded for an index of aggression. The number of alders (Alnus glutinosa and A. incana) preferred by hazel grouse for foraging was determined for each seasonal territory as described in Chapter VII.

Throughout this chapter, the means are presented with the standard error of the mean. When a 2x2 contingency table was used to test for differences in frequency data, the result was corrected for continuity with Yate's correction.

RESULTS

A total of 28 hazel grouse was captured and radio-marked during this study. At any given time, 60-100% of the territorial males and 33-100% of the territorial females were marked.

Timing of autumn territoriality

Spontaneous advertisement showed a very weak increase through the summer to November, a decline in December, and a sharper rise in late winter (Fig IV-1). Pynnönen (1954) recorded rates of response to imitation of the territorial song with a hunter's whistle in southern Finland, at about the same latitute as this study area. He found low response rates in summer, a clear peak in September and October, a decline through winter, except for a higher rate in December, and a rise in March (Fig. IV-1). Both of these data sets include mostly male advertisement. However, I recorded instances of spontaneous advertisements from radio-marked females, including two songs and four flutter jumps in autumn and one song and seven flutter flights in winter. Not included

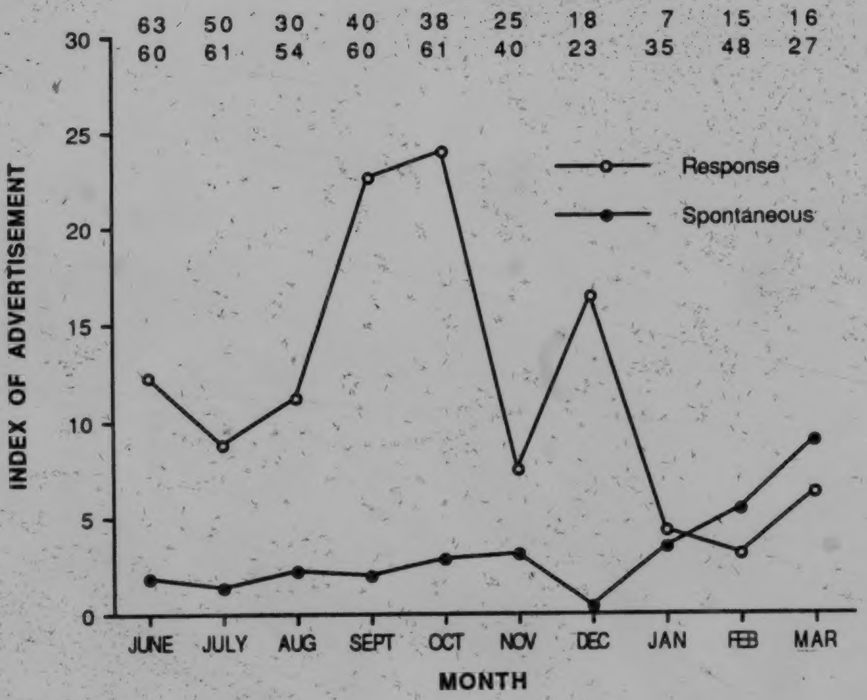

Fig. IV-1. Monthly indices of spontaneous territorial advertisement on the study area (instances per 10 field days) and of responses to an imitation of the territorial song (instances per 5 field days) in southern Finland (from Pynnönen 1954:69) during the nonbreeding season. Numbers are field days for responses (above) and spontaneous (below) data.

are many instances of females singing when separated from a male or chicks following disturbance.

New males in a territory advertised spontaneously more often (0.13±0.01 instances per relocation during September-November, N=2 males) than established males (0.03±0.01, N=11; Mann-Whitney test, U=22, df=12 males, P=0.027). The rate of spontaneous advertisement for established males did not vary significantly with the annual survival rate within their territories, a measure of habitat security, see Chapter VIII, (r_s=0.119, df=9, p=0.71).

Very few border disputes were noted among males until August, a peak occurred in October and November, an intermediate level was seen in December, with none observed after that (Fig IV-2). Females participated at a low level in October and November and at a higher level in December (Fig. IV-2). But, given the sample sizes of females, the pattern was similar to that of males. The females involved in the two disputes in October were accompanying males in border disputes, but the six instances in November and December were female-female border disputes.

Patterns of activity rates were similar for males and females; low in July and August, a peak in September and October, and a sharp decline to December or January, followed by an increase towards the breeding season (Fig. IV-3). Distance moved from one day to the next also showed a rather similar pattern for males and females, with low but increasing rates through summer, an autumn peak, and intermediate levels in winter (Fig. IV-4). However, the male peak occurred sooner (September) and was sharper than the female peak, which was greatest in October and lasted from September through November.

Size and spatial arrangement of territories

Territory size was similar for males and females in both summer (t=1.28, df=18, P=0.22) and autumn (t=0.27, df=20, P=0.79, Table IV-1). Therefore, the sexes were combined to test for differences in size between seasons. Summer territories were over 50% larger than autumn territories (t=2.49, df=39, P=0.02). No differences in size were found between territories of adults and yearlings in summer (t=1.05, df=18, P=0.31) nor between adults and juveniles in autumn (t=0.19, df=20, P=0.85). In winter, female territories were larger than male territories (Chapter VII), but neither female territories (t=1.21, df=13, P=0.25) nor male territories (t=0.28, df=26, P=0.78) changed significantly in size from autumn to winter.

Territory sizes, sexes combined, were compared with alder density within each territory and the population density on the study area in both autumn and winter using a stepwise multiple regression. In autumn, only population density was entered into the regression for all birds (F=12.68, df=1,19, one-tailed P=0.001) and for adults only (because juveniles had fewer alders in their territories, presented later) (F=10.20, df=1,17, one-tailed P=0.005). Alder density was unimportant in both cases (F=0.67, df=1,19, one-tailed P>0.25, and F=0.74, df=1,17, one-tailed P>0.25, respectively). In winter, although alder density was the only factor entered (F=11.27, df=1,18, one-tailed P=0.001), the

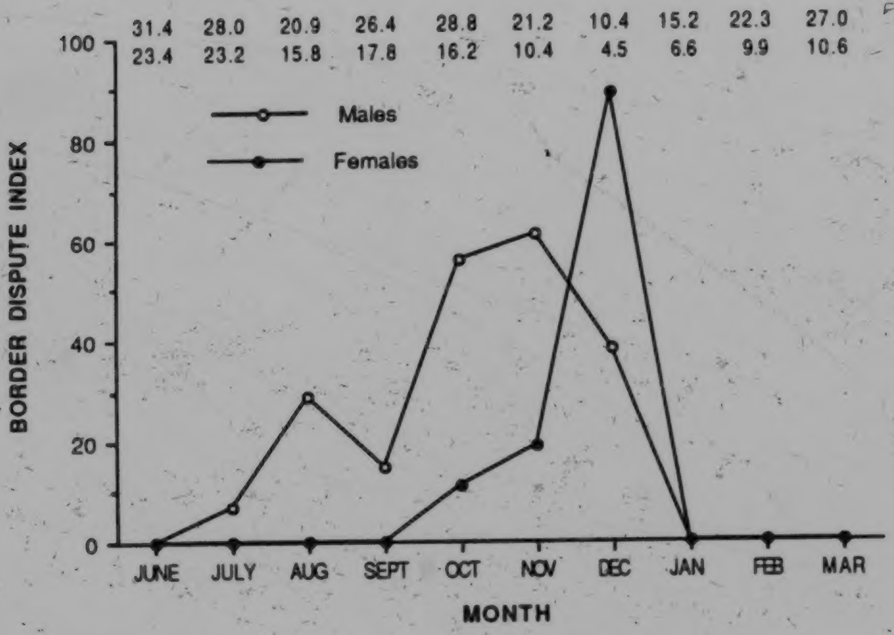

Fig. IV-2. Monthly indices of border disputes by radio-marked male and female hazel grouse on the study area during the nonbreeding season. (Indices were the number of border disputes divided by the product of radio-marked birds of each sex available that month times the number of months in the field [days÷30].) Numbers are this product for males (above) and females (below).

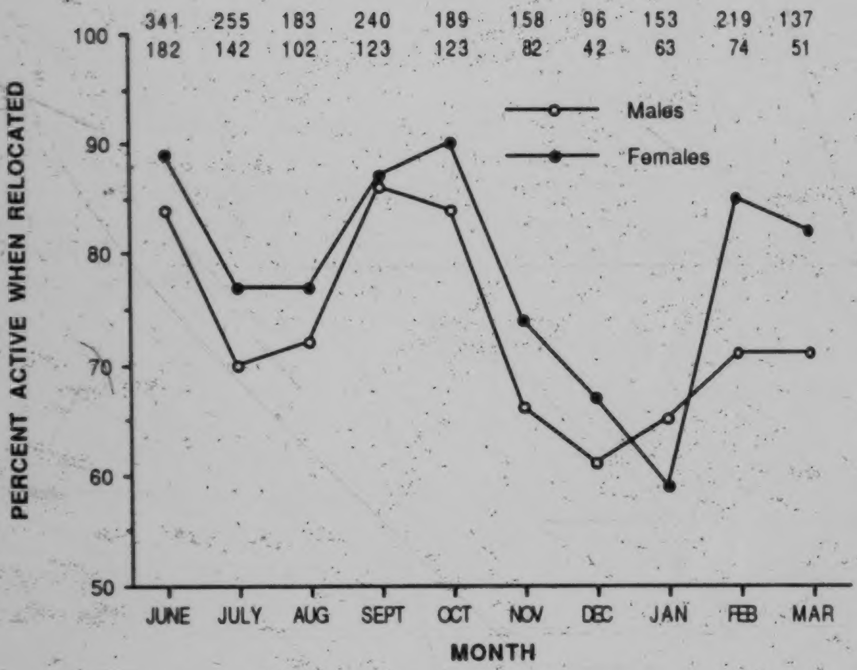

Fig. IV-3. Monthly indices of activity of radio-marked male and female hazel grouse on the study area during the nonbreeding season. Numbers are sample sizes for males (above) and females (below).

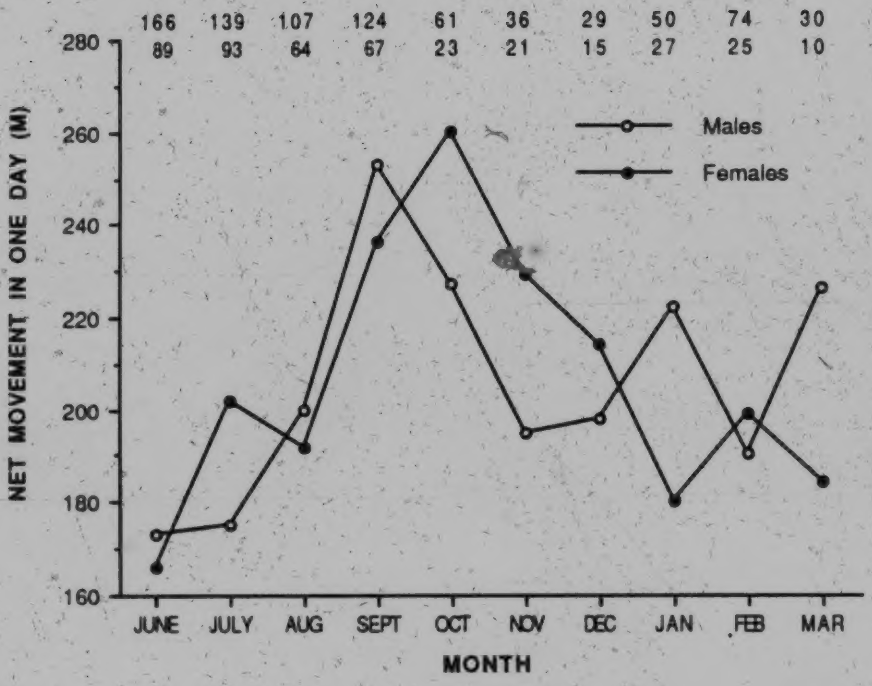

Fig. IV-4. Monthly rates of movement of radio-marked male and female hazel grouse on the study area during the nonbreeding season. Movement rate was the mean distance between relocations on two consecutive days. Numbers are sample sizes for males (above) and females (below).

Table IV-1. Size and mean overlap of territories of radio-marked male and female hazel grouse on the study area during summer, autumn, and winter. (Mean overlap is the mean of the overlap, in percent, of each of two neighbors of the same sex on each other's territory.)

		Season		
Variable	Sex	Summer	Autumn	Winter
Size (ha)	Males	22.9±2.7 (11)[a]	17.2±2.3 (13)	16.4±1.6 (14)
	Females	30.9±6.3 (8)	18.2±2.9 (8)	22.5±1.4 (6)
	Combined	26.3±3.1 (19)	17.5±1.7 (21)	18.2±1.3 (20)[b]
Overlap (%)	Males	20.8±7.8 (8)	7.2±3.4 (11)	6.1±2.6 (9)
	Females	16.9±9.1 (5)	0.9±0.9 (7)	1.4±0.9 (4)
	Combined	19.3±5.7 (13)	4.7±2.2 (18)	4.6±1.9 (13)

[a] Mean±SE (N), for overlap, N=number of pairs of neighbors.
[b] Included for completeness, male and female territories differed in size.

improvement of the regression obtained by adding population density bordered on statistical significance (F=3.55, df=2,17, P=0.052), and I argue that it was biologically significant. Together in a multiple regression, these two factors explained almost half of the variation in size of winter territories (r^2=0.49, df=18, one-tailed P=0.002). No accurate estimates of population density were available for summer.

A seasonal pattern similar to that found for territory size was evident in mean territory overlap between neighboring grouse of the same sex (Figs. IV-5, 6 & 7). Amount of territorial overlap with birds of the same sex did not vary between sexes in either summer (U=23.5, df=12, P=0.60), autumn (U=54, df=17, P=0.11), or winter (U=23, df=12, P=0.43, Table IV-1), so sexes were combined to test for differences among seasons. Mean territory overlap with a neighbor of the same sex varied significantly among seasons (Kruskal-Wallis test, H=7.88, df=2, P<0.025). Territory overlap was over four times greater in summer than in autumn (U=179.5, df=30, P=0.009), but there was no change from autumn to winter (U=136.5, df=30, P=0.40). Territorial overlap between neighbors of the same sex was low in autumn and winter; territories were virtually exclusive (Table IV-1).

Mean territory overlap between consecutive seasonal territories for the same individual was relatively high, from 37-61% (Table IV-2). There was no significant difference between sexes in amount of overlap of seasonal territories (U values varied from 12-42, P values from 0.27-0.67), so sexes were combined to test for seasonal differences, but none was found (H=7.04, P>0.05). The mean overlap between consecutive winter territories for four males and one female was 47±9%, showing the sedentary nature of hazel grouse on the study area.

Degree of territory overlap appeared to be partially a function of territory size. The amount of overlap with a male's nearest neighbor was correlated with the size of that male's territory in winter (Spearman rank correlation, r_s=0.621, df=11, P=0.04, Fig. IV-8). This relationship appeared to be linear. In a stepwise multiple regression, only size was entered as a significant variable (F=6.91, df=1,12, P=0.025); the square of size did not improve the relationship (F=0.004). No such relationship was found in autumn (r_s=0.127, df=11, P=0.66). A review of the locations of neighbors in winter showed that "overlap" occurred when a holder of a large territory was far from the intruder's territory. This was in contrast to the situation in summer, when an intruder sometimes was with a "territory holder" within his territory. Males were used for these tests because of greater sample sizes and greater variation in overlap (Table IV-1).

Indications of territorial aggression

The territorial behavior of male hazel grouse is well known. My results showed that 80-85% of the territorial males in an area responded to an imitation of the territorial song (hunter's whistle) within six minutes in both autumn and spring (Swenson 1991). However, no data have been published on the response of females to aggressive calls.

Ten tests with an imitation of the hen call were conducted on radio-marked

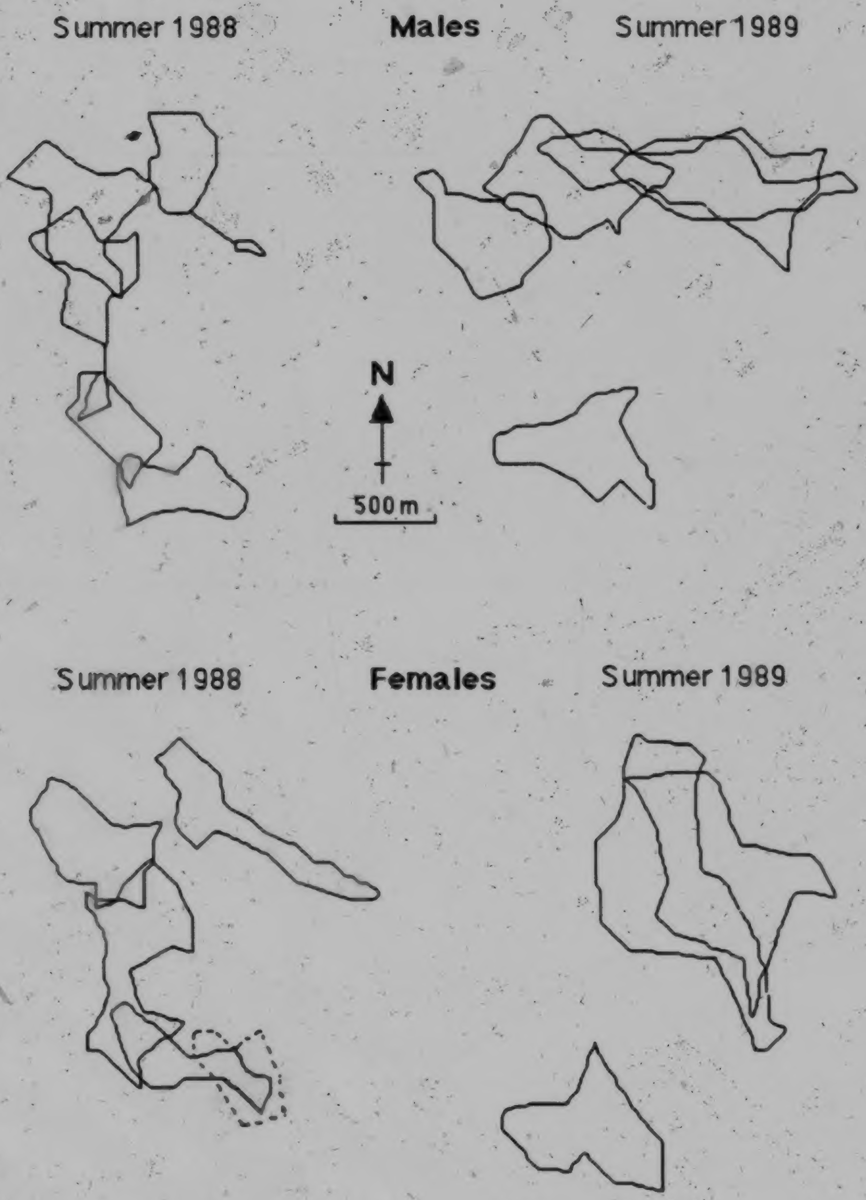

Fig. IV-5. Map of territorial boundaries of male and female hazel grouse during summer on the study area. (The dotted line shows a territory that did not have enough points to be included in the data set.)

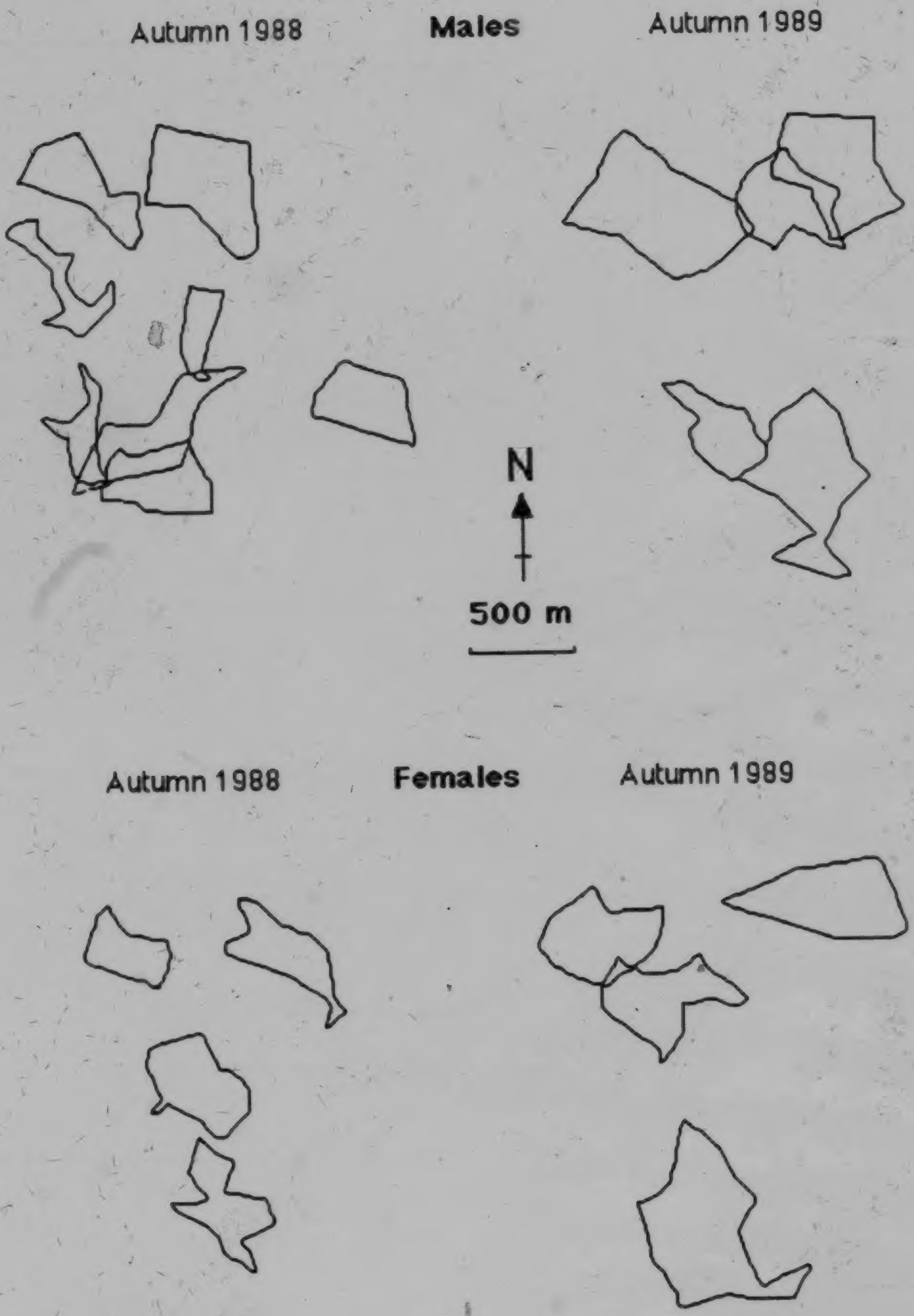

Fig. IV-6. Map of territorial boundaries of male and female hazel grouse during autumn on the study area.

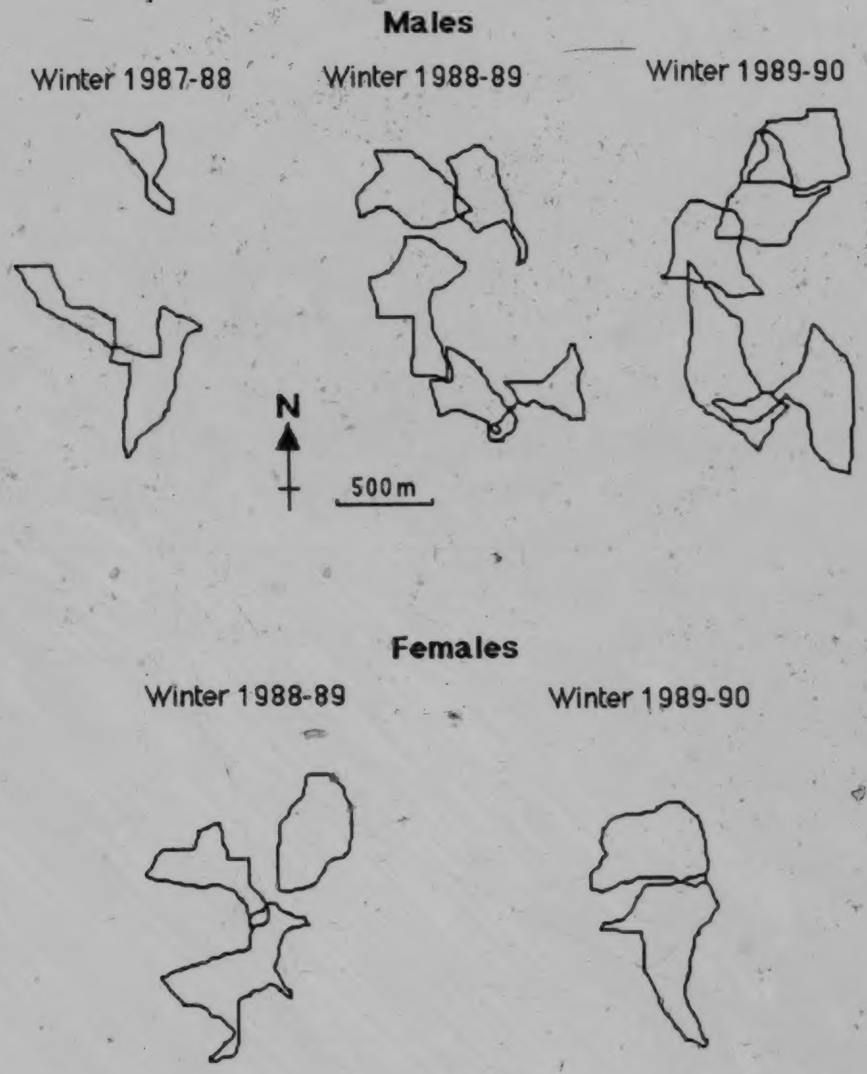

Fig. IV-7. Map of territorial boundaries of male and female hazel grouse during winter on the study area.

Table IV-2. Degree of overlap of seasonal territories of individual hazel grouse on the study area (overlap is defined as the percentage of the first seasonal territory that is included within the second seasonal territory). Data from three males were that left the study area are excluded for the periods they were gone, but data from birds changing territories within the study area are included.

	Degree of overlap between seasons			
Sex	Winter-spring	Spring-summer	Summer-autumn	Autumn-winter
Males	58±10 (10)[a]	42±7 (9)	61±5 (9)	47±7 (12)
Females	78±12 (2)	21±16 (3)	47±9 (7)	39±8 (5)
Combined	61±8 (12)	37±7 (12)	55±5 (16)	45±5 (17)

[a] Mean±SE (N).

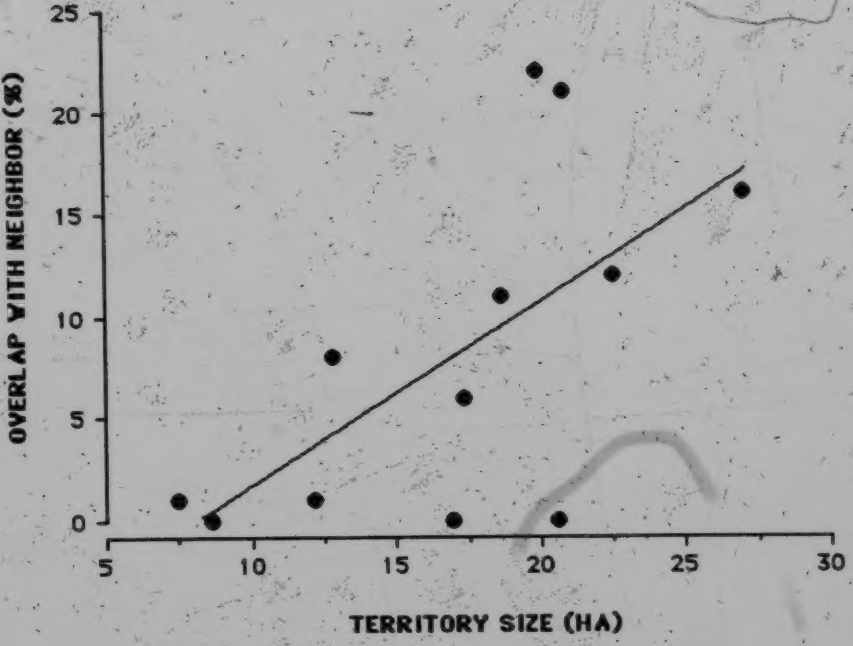

Fig. IV-8. Relationship between degree of territory overlap with nearest neighbor and winter territory size for males on the study area (r_s=0.621, df=11, P=0.04).

territorial female hazel grouse in autumn (Table IV-3). In eight of these, the female approached me, even as close as 10 m and, in one case, a female moved 280 m away from me to the male in the territory. Only one female showed no response, moving neither closer nor further. It was aware of my presence prior to the test, which may have affected its subsequent behavior. During these tests, two or three females responded with aggressive advertisement, including the hen call, flutter jump, flutter flight, and "Plittern", a call of agitation (Scherzinger 1981). Some of these responses were dramatic. One female answered with a hen call immediately, flew 95 m in 38 sec, flutter-jumped, and called with the "Plittern" only 15 m from me. Another one flew with a flutter flight to a tree within 10 m of me and gave the hen call. This was the only female I saw during these tests; more commonly the females approached quietly. No females attacked the mounted female.

The one female that showed a clear negative reaction to the hen call, moving 280 m away from me (bird 395, Table IV-3) had been marked only six days prior to the test and died 13 days afterwards. Although it was located in the vicinity of the test site only on the day of the test, it was not possible to determine if it had been outside its territory when the test was performed.

It appeared that two radio-marked adult males attempted, but failed, to establish autumn territories in alder-rich areas already occupied by radio-marked territorial birds. They ceased their efforts on about 16 and 27 November, respectively. Both radio-marked juvenile hazel grouse established territories in the autumn. They entered their territories three days (a male) and seven days (a female) after leaving their mothers on 12 and 19 September, respectively (Swenson in press). Juveniles may be less aggressive in defending their territories than adults. All 10 hazel grouse I captured in the autumn, primarily using the whistle to lure them into a net or keep them in the area long enough to chase them into the net, were adults, compared with seven adults of 16 birds in the spring ($\underline{X}^2_c$=6.30, df=2, P=0.012).

There was no evidence that territorial aggression changed with density during this study. Although the autumn population declined ca. 75% during this study, there was no significant change in response time to the imitated territorial song during autumn censuses (ANOVA, F=0.9, df=3, P=0.97, Table IV-4). The spring population declined ca. 67% during this study.

Replacements in territories following their vacancy

Timing of territory occupation by a new hazel grouse following the death or emigration of a radio-marked territory holder was similar for males and females (Fig. IV-9). Periods of two to three months were grouped to search for patterns because of small sample sizes. No territories were known to be acquired during May-July. The rate of acquisition of vacant territories increased to 17% per month in August-September and 100% per month in October-November for both sexes. A territory acquisition rate of 100% meant that each vacant territory was filled in October, and all those becoming vacant in November were filled that month. During December-April, acquistion rates were 33-50% per month for both sexes (Fig. IV-9). Territory acquisiton in October-November was 100%

Table IV-3. Responses of territorial female hazel grouse to an imitation of the aggressive hen call in autumn.

Bird No.	Date	With male?	Distance from me Start	Distance from me Stop	Dist. moved[a]	Vocalizations[b]
389	4 Oct 88	Yes	50	25	+25	
387	6 Oct 88	No	60	60	45	
390	6 Oct 88	No	50	25	+25	
388	7 Oct 88	Yes	60	10	+50	
395	26 Oct 88	No	40	280	-280	
390	25 Sept 89	No	100	60	+75	
399	25 Sept 89	Yes	110	15	+95	H, Fj, P
396	6 Oct 89	No	55	10	+45	H, Ff
401	12 Oct 89	Yes?	150	45	+145	Fj?
403	18 Sept 89	No	45	30	+>50[c]	

[a] +=moved towards me, -=away, no sign= no change, distances in m.

[b] H=hen call, Fj=flutter jump, Ff=flutter flight, P="plittern".

[c] Circled around me.

Table IV-4. Censuses of territorial male hazel grouse in autumn and spring on the study area (195 ha of forest) and response time to the imitation of the territorial song in autumn

Year (Autumn)	Density of males (N/100 ha) Autumn	Density of males (N/100 ha) Next spring	Response time (min) mean±SE (N)	
1987	8.2	4.6	3.22±0.45	(20)
1988	5.6	2.6	3.40±0.49	(14)
1989	2.6	2.1	2.95±1.19	(5)
1990	2.1	1.5	3.55±1.18	(5)

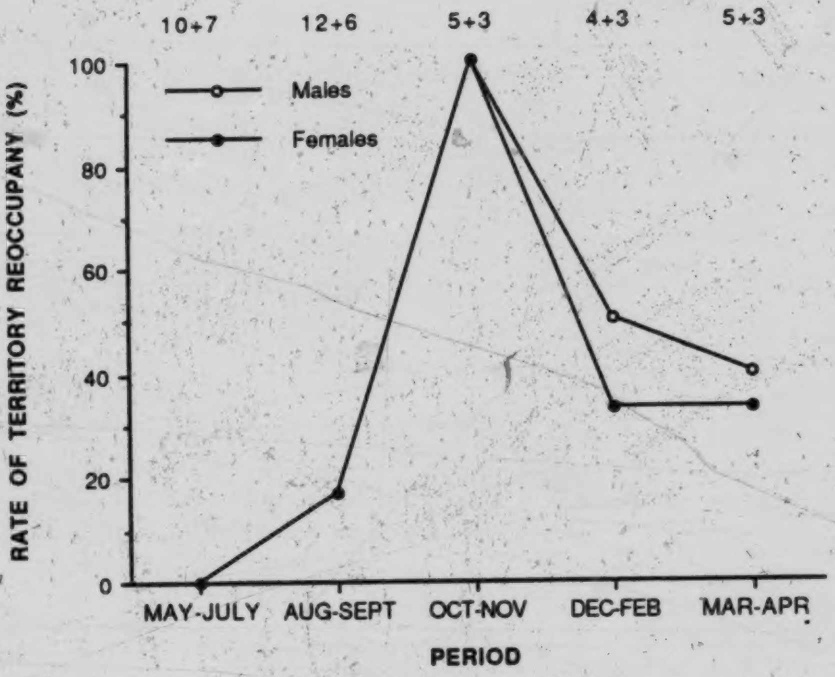

Fig. IV-9. Rates of known territory acquisiton following the death or emigration of a radio-marked territorial hazel grouse throughout the year on the study area. Numbers are the number of territories vacant during a month (male+female).

in spite of the declining population because some birds occupied territories later in the study that had been divided among two birds earlier.

Ages of known-age birds acquiring territories on the study area (either radio-marked birds or birds captured later, sexes combined) were: one adult and three juveniles in September, three adults and two juveniles in October-November, two juveniles in December-February, and two adults and one yearling in March-April. Four radio-marked birds changed territories within the study area, two adult males and two adult females. Two of these changes (one male and one female) occurred between winter and spring; the other two occurred at the beginning of autumn. Three involved movements to a neighboring territory that became vacant; the fourth was a movement of 1 km (between territory centers). Five male grouse left the study area in late winter and spring, but those that survived returned in autumn (Chapter II). Territory reoccupancy was rapid when openings occurred in October- November; mean maximum time for replacement was 5.7±2.0 days (N=3).

Variation in territory quality

Survival. There was considerable and significant variation in annual survival rates among territories, from 8-100%. The difference in seasonal survival rates between secure and insecure areas was greatest, and only statistically significant, in early winter (early November to mid-January), when 0 of 12 birds died in the secure areas, compared with 7 of 15 (47%) in the insecure areas (Table VIII-3). Variation in survival rates was correlated with variation in forest structure (Chapter VIII).

Reproductive success. Too few data were available to determine if reproductive success varied spatially. However, females tended to be more successful in hatching a clutch in areas with the highest survival (50% successful, N=8, generalized territories A-E and I, Fig. VIII-2) than in areas with the lowest survival (none successful, N=5, in territories F-H; $0.2<P<0.1$, one-tailed Fisher's exact test).

Winter food resources. Alder constituted the most important winter food resource for hazel grouse in this area, and hazel grouse distribution and density was related to alder distribution and density at several levels of scale. Alder trees >10 m high and ≤15 m from spruce forest were preferred for foraging (Chapter VII).

No difference was found in the number of preferred alders between male and female territories in summer (U=42, df=18, P=0.86), autumn (U=62, df=20, P=0.47), or winter (U=59, df=18, P=0.16, Table IV-5). Therefore, sexes were combined to test for seasonal and age differences. The number of preferred alders within territories did not change significantly from summer to autumn (U=188, df=36, P=0.60), but increased from autumn to winter (U=285.5, df=38, P=0.008, Table IV-5). The territories of juvenile hazel grouse were excluded from these tests, because their autumn territories contained significantly fewer preferred alders (0.8±0.9, N=2) than adults (97.5±12.8, N=19, U=38, df=20,

Table IV-5. Number of preferred alders within territories of male and female hazel grouse on the study area in summer, autumn, and winter. (A preferred alder is ≥10 m tall and ≤15 m from spruce cover.)

	Season		
Sex	Summer	Autumn[a]	Winter
Males	114±26 (10)[b]	104±17 (12)	136±14 (14)
Females	107±23 (8)	86±20 (7)	161±16 (6)
Combined	111±17 (18)	98±13 (19)	144±11 (20)

[a] Excluding juveniles.

[b] Mean±SE (N).

P=0.023). The density of preferred alders was not correlated with annual survival within generalized territories (Chapter VIII).

Seasonal changes in population size

Because this was an intensive study of social organization, I was not able to gather data on seasonal changes in population size over an extensive area. Therefore, I analyzed data presented by Gavrin (1969). He censused hazel grouse three times a year (spring, 27 March-10 April; summer, 25 July-10 August; autumn 10-20 October) along 180 km of permanent transects during five years in the Bialowieza old-growth forest on the border of Belorussia and Poland. Gavrin (1969) did not analyze these data with respect to population regulation, nor did Leclerq (1988) cite them.

Gavrin's (1969) data showed no relationship between numbers of hazel grouse observed in summer and the following autumn (r^2=0.005, df=2, P=0.93), or summer and the following spring (r^2=0.014, df=2, P=0.88). There were, however, tendencies towards positive relationships between decline in counts from summer to autumn and summer numbers (r^2=0.71, df=2, one-tailed P=0.08, Fig. IV-10) and between decline in counts from summer to spring and summer numbers (r^2=0.52, df=2, one-tailed P=0.14). The tests were one-tailed because the direction was predicted from Leclerq's (1988) results. Summer counts showed higher variation (CV=30%) than autumn counts (CV=11%, F=21.8, df=4,3, P<0.02, Fig. IV-11), suggesting that regardless of the number of young produced in a given summer, the population returned to about the same level prior to mid-October each year.

DISCUSSION

Social organization

Both male and female hazel grouse maintained territories in autumn through winter that satisfied the classical definition of territoriality, ie. defense of a fixed area and exclusion of conspecifics (Brown & Orians 1970), in this case conspecifics of the same sex. This was the first documentation that female hazel grouse are territorial at this time and that either sex actually defended fixed, exclusive territories. Singing by females has been recorded in the wild (Pynnönen 1954), although Scherzinger (1981) did not observe it in captivity. To my knowledge, this is also the first documentation of spontaneous flutter flights and flutter jumps, and the reaction of territorial females to the hen call. The females' reaction to the hen call was similar to males' reaction to the territorial song in autumn, by approaching and advertising. However, advertisement was more common for males (91%, Swenson 1991) than females (20-30%, Table IV-3). Females did not attack the mounted female, as do females of some North American species (Hannon 1983, Bergerud & Butler 1985, Martin et al. 1990). However, male hazel grouse do not attack mounted males either (Klaus et al. 1975, pers. obs.).

Both sexes exhibited a low level of territorial behavior in summer (Fig. IV-12). Territories were large and territory overlap was relatively high (Tables IV-1 & 2, Fig. IV-5), activity and daily movement rates were low (Figs. IV-3 & 4),

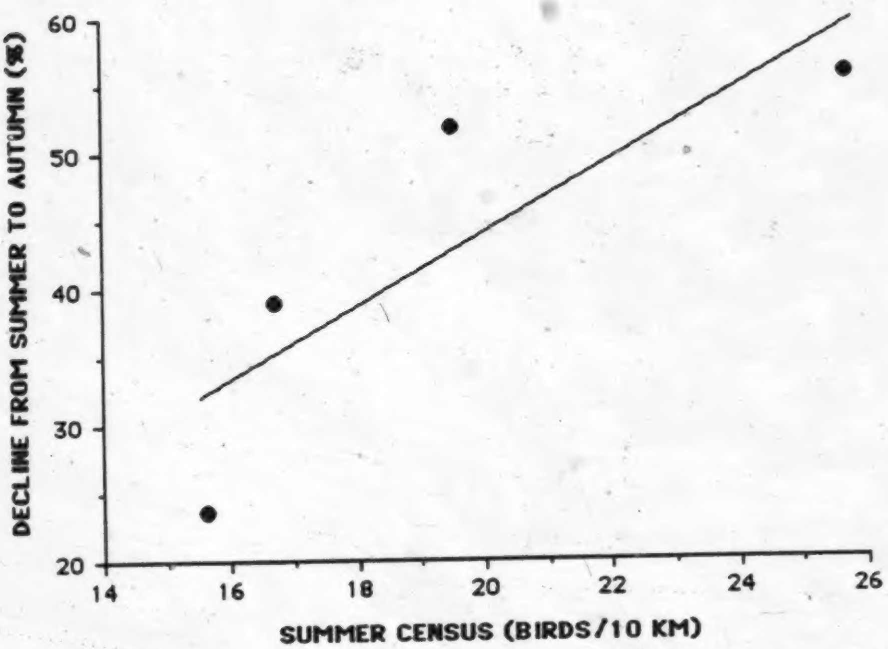

Fig. IV-10. Relationship between decline in hazel grouse counts from summer to autumn and summer counts, based on line transects, in the Bialowieza Forest, Belorussia, during 1948-51 (r^2=0.52, df=2, one-tailed P=0.14, data from Gavrin 1969).

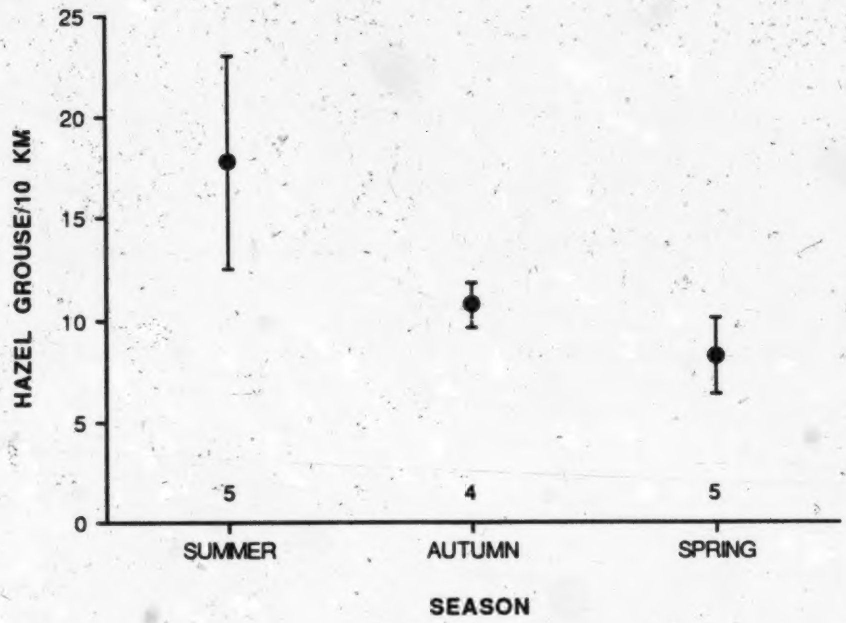

Fig. IV-11. Means and variation (standard deviation) of hazel grouse counts based on line transects during three seasons of each year, 1948-51, in the Bialowieza Forest, Belorussia, during 1948-51 (data from Gavrin 1969). Numbers are sample sizes (seasons).

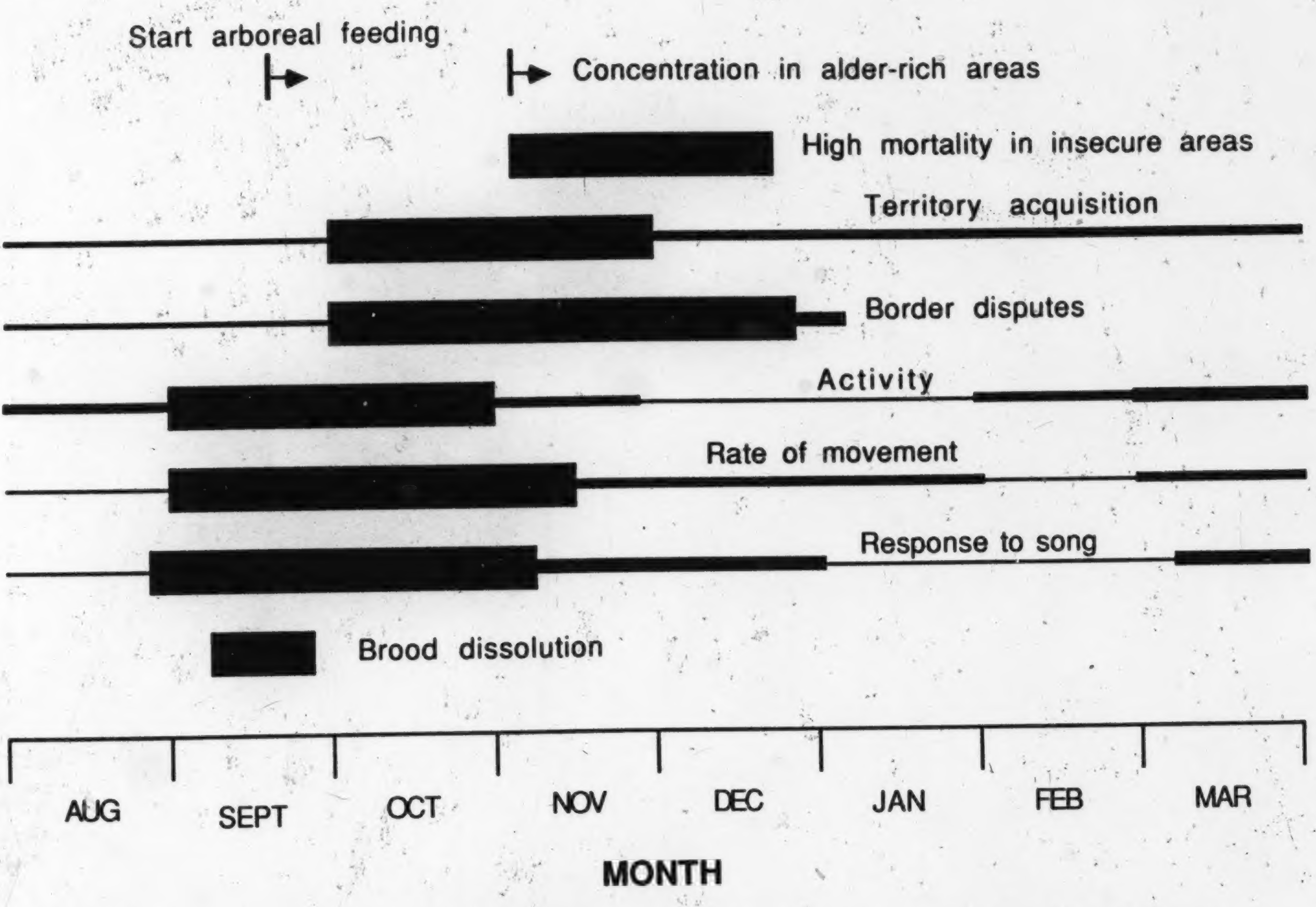

Fig. IV-12. Summary of timing of important events in the social organization of hazel grouse during August through March. The intensity of the event is shown by the thickness of the line.

there were few border disputes (Fig. IV-2), virtually no vacant territories were occupied (Fig. IV-9), and there was a low response rate to imitations of the territorial song (Pynnönen 1954, Fig. IV-1). Hazel grouse appear to be nonterritorial during summer, from hatching in June through most of August. Thus, it is more correct to refer to home ranges rather than territories during this time. This contradicts the widely-held opinion that hazel grouse are territorial year-long (Pynnönen 1954, Klaus et al. 1975, Zbinden 1979).

Territoriality began again abruptly in late August-early September (Fig. IV-12). This was characterized by greater responses to imitation of the territorial song (Fig. IV-1) and increased rates of activity and movement (Figs. IV-3 & 4). Also, territories were smaller and overlapped less in September-October than in summer (Tables IV-1 & 2, Fig. IV-6). Pynnönen (1954) recorded the hen call more often in autumn than in spring, especially from early September to the end of October. The beginning of territorial behavior must have involved adults reclaiming their territories or moving to new ones.

Juveniles establish territories during their first autumn (Klaus et al. 1975, Scherzinger 1982, Potapov 1985, this study), but brood dissolution on my study area occurred mainly during the second and third weeks of September, two to four weeks after the adults became territorial (Fig. IV-12). Two radio-marked juveniles from different broods entered their future territories three and seven days after leaving their mothers on 12 and 19 September, respectively. About this time, during October and November, filling of vacant territories and border disputes reached peak levels (Figs. IV-2, 9 & 12). This suggested that many territories were filled by juveniles during this period. This was not documented directly, because I was not able to capture juvenile territory-holders in the autumn. However, adults were also involved, as shown by the two radio-marked adults that tried unsuccessfully to expand their territories into other radio-marked birds' territories and the documented changing of territories by two territorial radio-marked birds at this time. That juveniles were more difficult to capture than adults in autumn using an imitation of the territorial song suggested that adults defended their territories more agressively than juveniles against a perceived intruder in the autumn.

Hazel grouse responded to the whistle at a relatively greater rate than they advertised spontaneously during autumn and early winter (Fig. IV-1). This may be because hazel grouse songs are individually recognizable, and males react much less to their neighbor's song than to that of an intruder (Bergmann et al. 1975). However, rate of spontaneous advertisement was related to the male's tenure on the territory, with new occupants advertising over four times more often than established occupants. Much of hazel grouse behavior appears to be an adaptation to avoid attracting predators (Scherzinger 1981) and, although the territorial song is acoustically cryptic within the dense coniferous forest that constitutes hazel grouse habitat (Bergmann et al. 1975, Hjorth 1976), spontaneous advertisement may attract a predator's attention and increase the chance of predation. I have seen a pine marten (Martes martes) come to a hunter's whistle, and others have told me that goshawks (Accipiter gentilis) do the same. Both are important hazel grouse predators (Chapter VIII). Perhaps a tradeoff is involved; birds may advertise only enough to announce their possession of a territory. Advertisement of possession is probably more important for a new occupant.

Territorial activity declined during the winter, with some resurgence at the end of winter, towards the spring territorial period (Fig. IV-12, Chapter II). However, the low level of territory overlap in winter (Table IV-1, Fig. IV-7) indicated that territories were maintained even then. The degree of intrusion into a territory by the neighbor (a measure of cost of territorial defense) increased linearly with territory size, as predicted by MacLean & Seastedt (1979). Hazel grouse appeared to have difficulty effectively defending an exclusive territory when the size exceeded about 20 ha (Fig. IV-8).

The sedentary nature of territorial hazel grouse on the study area was shown by the high degree of overlap between seasonal territories (Table IV-2) and winter territories in subsequent winters. Five adult males left the area for spring and summer, and all three survivors returned in the autumn (Chapter II). In contrast, several unmarked adults moved into vacant territories on the study area. Thus, there was a net movement of adults into the study area. Perhaps the habitat on the forest reserve was better than that in the surrounding managed forest, and adults changed territories to gain a better one.

In summary, both male and female hazel grouse defended territories from other members of the same sex during autumn and winter. From the timing of behavioral events (Fig. IV-12), it is apparent that juveniles began searching for territories after the adults were established, and therefore must have been forced to establish territories in areas not chosen by adults.

What is being defended?

Brown (1964a) maintained that intraspecific aggression was a behavioral response to competition for ecological requistes in short supply. The data suggested that winter food, especially within forest with good survival qualities, was important. This is commonly defended by birds (Brown 1964a). Territory size was correlated with population density, but not winter food abundance, in autumn and with both winter food density (more important) and population density in winter. The results from winter suggested that a food resource was defended from competitors (Brown & Orians 1970, Hixon 1980, 1987, Gauthier 1987, Schoener 1987). Autumn territories of juveniles contained only a small fraction of the number of preferred alders found in adult territories. Territories shifted somewhat from autumn to winter, not in size (Table IV-1), but in space (Table IV-2), so that winter territories contained more alder trees of the size and proximity to spruce cover preferred by hazel grouse for foraging (Table IV-5). Perhaps this was because cowberries and billberries (Vaccinium vitis-idaea and V. myrtillus) were important autumn foods (Ahnlund & Helander 1975), and they do not grow in conjunction with alders (Chapter VII). The high overlap between seasonal territories throughout the year showed that hazel grouse defended areas with preferred alders in other seasons also (although this was probably not the resource defended at the time), but did not concentrate in these areas until winter. Further support for the conclusion that winter food was an important defended resource was found in the high preference for alder as a winter food, its relative scarcity, and relationships between the distribution and density of hazel grouse and alder on several levels of scale (Chapter VII). In Siberia, where food apparently was not limited, hazel grouse did not defend winter territories, but overwintered in flocks (Chapter VI).

Autumn territoriality and population regulation

Fretwell & Lucas (1970) stated that territoriality would result in the regulation of population size if some individuals monopolized the best habitats and forced others into less suitable habitats, an ideal despotic distribution of individuals (Fretwell 1970). They proposed that this would be the case if birds in habitats with high density could be shown to have higher success than those in habitats of low density. If there were no differences, the distribution was ideal free, and territoriality would not be a factor in population regulation. However, population density is not necessarily an accurate measure of habitat quality (Van Horne 1983); it is sufficient to show that there is a spatial heterogeneity in the suitability of habitats and that there is an unequal resource partioning among individuals (Lomnicki 1978, 1980, 1988, Andrén 1990).

The hazel grouse population on my study area met the criteria of an ideal despotic distribution. They were territorial, with unequal resource partitioning among individuals, and spatial heterogeneity of habitat quality. Territorial behavior began in the autumn, and an important defended resource appeared to be alder, the most preferred winter food. Juveniles established territories during their first autumn in areas with few alders that were not chosen by adults. The area was heterogenious with respect to both winter food dispersion and survival (Chapters VII & VIII). Survival rates varied greatly within the study area, and was related to forest structure. Because hazel grouse showed high site fidelity, birds in secure habitats usually remained there, and the vacant habitats available to juveniles were usually the dangerous ones. Thus, adults were the despots, as has been found in other species of resident territorial birds (Andrén 1990, Enoksson 1990). The social organization and resulting population regulation observed in hazel grouse was quite similar to that found in the nuthatch (Sitta europaea), another species that defends long-term territories containing a nonrenewing food supply (Enoksson 1990).

The difference in survival between secure and dangerous territories was greatest in early winter (early November to mid-December), when 47% of the radio-marked birds in dangerous territories were killed (Chapter VIII). This is after territory establishment by juveniles. The lower rates of territory acquisition following the early winter mortality peak (Fig. IV-12), suggested that there was no surplus of nonterritorial birds. At least during this study, mortality in the suboptimum habitats during early winter seemed to be sufficiently high to prevent a surplus population of floaters from forming (Brown 1969b). This suggests that the upper density of hazel grouse in an area should be determined by the amount of spruce forest with a secure structure that contains enough alder to support winter territories. The limitation of numbers of territorial hazel grouse appeared to be a secondary consequence of a combination of some other primary benefit to the individuals, ie. defense of winter food (Brown 1969a), and the spatial heterogeniety in likelihood of survival (Lomnicki 1978, 1988). As concluded in Chapters VII and VIII, heterogeniety in dispersion of winter food and survival appears to be a general feature of hazel grouse habitat. Thus, the results of this study should be applicable to hazel grouse populations generally. This and the finding that hazel grouse are more vulnerable to goshawk predation during high population levels, when they are more common in less-preferred habitats (Lindén & Wikman 1983), support Leclerq's (1988) hypothesis that autumn territoriality in hazel grouse results in regulation of population size. However, this may not occur in areas where they form flocks in winter and do not exhibit territorial behavior in autumn and winter (Chapter VI).

Based on a limited data set, Leclerq (1988) proposed that the regulation of numbers of hazel grouse by territoriality occurred during the autumn period of territorial advertisement in France. In Sweden, spacing of individuals occurred then, but the regulation of numbers, ie. mortality in less secure territories, occurred primarily in early winter, after the peak of territorial behavior. However, data from Belorussia (Gavrin 1969, Fig. IV-11) suggested that regulation there occurred before mid-October. Thus, either the results from France and Belorussia were due to emigration from the study areas, or the period of high mortality in less secure habitats occurs at different times in different areas.

The available data did not support Bergerud's (1988) hypothesis that changes in spring numbers were caused by breeding success the previous year. There was no correlation between numbers of hazel grouse in summer and the following autumn or spring in Gavrin's (1969) five-year study. Similarly, there was no correlation between reproduction in year x and change in the adult population from year x to year x+1 during 11 years in France ($r^2=0.05$, df=8, P=0.53, data from Leclerq 1988:279). The transect method used in both of these studies is efficient in finding grouse broods (Brittas & Karlbom 1990).

No experiments were performed during this study because the social organization had not been documented previously. The available evidence supported the hypothesis that autumn territoriality resulted in population limitation. This hypothesis should be tested by removing territory-holders before, during, and after the October-November period of territory acquisition. Neighbors of the bird to be removed should be radio-marked, along with as many juveniles as possible in the area while they are with their mothers (and easier to capture) to gather data on territory acquisition by juveniles. Also, alders should be removed to test if they are really the key resource being defended. Age ratios in the hunter harvest could be examined to determine if the proportion of juveniles declines rapidly during early winter, as this hypothesis predicts high juvenile mortality at this time.

Population regulation and population stability

The proposed system of intrinsic population regulation in hazel grouse predicts relatively stable numbers after regulation has taken place, as long as habitat quality remains stable (Lomnicki 1980). In fact, autumn numbers were stable over four years in Belorussia (Fig. IV-11) and adult densities were quite stable over 11 years in France (Leclerq 1988:281). However, hazel grouse numbers vary cyclicly farther north, following 3-4 year cycles in Scandinavia, northernmost Finland, and Soviet Lapland (Semenov-Tyan-Shanskii 1959, Hörnfeldt et al. 1986, Lindén 1988), and 6-8 year cycles in most of the rest of Finland, in Soviet Karelia and near the Ural Mountains in European Russia (Jurgenson 1961, Lindén 1988). Population size in both spring and autumn was declining during my study (Table IV-4), even in the secure habitat. This suggested that either hazel grouse show a cyclic change in the spacing behavior (Watson & Moss 1979) in some parts of their range but not in others, or that an extrinsic factor is periodically imposed upon some populations that overrides the intrinsic system.

The hazel grouse population on my study area in autumn 1990 was only 26% of that counted in autumn 1987 and the size of territories in both autumn and winter were correlated with population density. This was consistent with Watson & Moss' (1979) hypothesis that cyclic grouse populations are a result of changes in spacing behavior and aggression. However, there was no evidence that increased territory size was due to increased aggression. The response time of males to an imitated song in autumn did not change during this study (Table IV-4). Similarly, no differences were found in response time in autumn among four areas with a 20-fold range in autumn densities (Swenson 1991). In addition, hazel grouse appeared less able to defend the largest winter territories, because territory overlap between neighbors increased with territory size (Fig. IV-8), supporting Huxley's (1934) concept of territories as compressed rubber discs. Thus, no support was found for the hypothesis that the observed decline in hazel grouse was caused by increased aggression leading to a greater spacing of territories.

An alternative hypothesis is that extrinsic factors caused the decline, probably through increased mortality of adults, nests, and/or young. The predator-switch hypothesis (Hagen 1952, Lack 1954), states that numbers of generalist predators build up as vole numbers increase, then switch to grouse, particularly nests and young, following the population crash of voles, and cause such high mortality that the grouse decline, after which the predators also decline. It is supported by correlative studies (Keith 1974, Angelstam et al. 1984, Keith & Rusch 1988, Lindén 1988, Steen et al. 1988) and experiments (Lindström et al. 1987, Marcström et al. 1988) in northern biomes. The observed decline on my study area was consistent with this hypothesis. Vole populations were high at the beginning of this study, they crashed in summer 1988, and were low through the rest of the study. Reproduction of all grouse species at Grimsö was low throughout this study (P. Angelstam, unpubl.). Also, the autumn censuses (Table IV-4) were made in mid-September to mid-October, prior to population regulation. This suggested that recruitment was insufficient to maintain numbers during this study. Further support for this hypothesis was the geographical coincidence of hazel grouse and vole cycles in northern areas of Fennoscandia and a lack of cycles in both grouse and voles farther south (Angelstam et al. 1985). Thus, within the areas of cyclic populations of hazel grouse, the size of hazel grouse populations following crashes in vole populations probably decline to levels lower than would be expected based on the amount of secure habitat with suitable winter food resources.

Comparison with other species of grouse

A powerful method for studying the general relationship between social organization and ecology is to compare groups of related species, especially if the group shows much variation in social organization (Krebs & Davies 1981). The subfamily of grouse (Tetraoninae) is closely related and exhibits a wide range of social organizations during the nonbreeding period (Wiley 1974). Hannon (1988) has concluded that intrinsic mechanisms of population regulation have not been adequately tested for grouse. Nevertheless, data supporting the hypothesis that territoriality is an important mechanism in population regulation have been found for several species: red grouse (*Lagopus lagopus scoticus*) (Jenkins et al. 1963, Watson & Jenkins 1968, Watson 1985), willow ptarmigan (*Lagopus lagopus*) (Hannon 1983, Pedersen 1988), rock ptarmigan (*Lagopus mutus*) (Watson 1965), spruce grouse (*Dendragapus canadensis*) (Herzog & Boag 1978, Boag & Schroeder 1987, Szuba & Bendell 1988), blue grouse (*Dendragapus obscurus*) (Bendell et al. 1972, Zwickel 1972, 1980, Hannon et al. 1982), and hazel grouse (this study). In most of these studies, spring territoriality was considered to be more important than autumn territoriality in regulating breeding numbers. Only in the red grouse and hazel grouse was autumn territoriality considered more important. There is also evidence that subadult male capercaillie (*Tetrao urogallus*) are excluded from some areas by adults in late winter (Gjerde & Wegge 1989), but the significance of this for population regulation was not addressed.

One of the emerging findings of sociobiology is that many aspects of an animal's social organization can be predicted on the basis of an understanding of a limited set of environmental variables (Emlen & Oring 1977). What do red grouse and hazel grouse have in common that is lacking in the other species? Red grouse, unlike hazel grouse, inhabit open moorlands dominated by heather (*Calluna vulgaris*). However, red grouse, like hazel grouse, are territorial from autumn through spring, territorial behavior is less pronounced during midwinter, and, although they are aggressive to members of the same sex, males and females are often together during the nonbreeding period (Jenkins et al. 1963, Watson & Jenkins 1964). This behavior is lacking, or is much less developed, in the other species mentioned above. Red grouse feed on heather almost exclusively within their territories during autumn and winter (Miller & Watson 1978, Lance 1978) and territory size is related to the content of nitrogen in the heather and diet (Lance 1978, Moss et al. 1988). Moss et al. (1988) concluded that red grouse were "food maximizers", obtaining as large a territory as possible to increase their choices of feeding sites because they are very selective feeders. Although heather is the dominant plant in red grouse habitat, it is much less nutritious than the winter diet of other subspecies of this bird (Moss et al. 1988). Hazel grouse are also selective feeders, showing high preference for a relatively rare food source in this area, alders ≥10 m tall and ≤15 m from spruce cover (Chapter VII). The winter diet of most grouse species consists of one or two food species that are dominant, or at least abundant, in the winter habitat (Doerr et al. 1974, Moss & Hanssen 1980).

In spring, when females require nutritious food for egg formation, red grouse females feed on heather, selecting territories and feeding sites with high nitrogen content (Moss et al. 1988). Hazel grouse females feed mostly on newly-sprouted forbs (Chapter III), which are associated with alder (Chapter VII), and are richer near alder because of the fertilizing effect of fallen alder leaves on the soil (Børset 1985). The other grouse species do not have such a close relationship between winter and spring foraging sites and species, except possibly ruffed grouse (Bonasa umbellus) and aspen (especially Populus tremuloides) (Gullion 1990).

Future research on the factors affecting the social organization of grouse in the nonbreeding season should test the hypothesis that territoriality is defense of the prospective value of limited food resources. Prospective value is defined as "the immediate value of the resource plus the cumulative value of that resource over the future period during which the resident can expect to use the territory" (Stamps & Tollestrup 1984:99). Here, the future period could include winter or winter and the prelaying period. This hypothesis predicts that territoriality will be stronger in species with limited winter food resources and strongest in species with limited winter food resources that coincide spatially with limited spring food resources. Population regulation as a result of autumn territoriality should be expected in these two groups. Tests should include comparisons of species that are and are not territorial in winter, and also populations within species that show variation in winter social behavior.

LITERATURE CITED

Ahnlund, H. & B. Helander. 1975. The food of the hazel grouse (Tetrastes bonasia) in Sweden. Viltrevy 9:221-240.

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay Garrulus glandarius L. Ecology 71:1796-1803.

Angelstam, P. K. 1988. Population dynamics in tetraonids: the role of extrinsic factors. Acta Congr. Intern. Ornithol. 19:2458-2477.

Angelstam, P., E. Lindström, & P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62:199-208.

Angelstam, P., E. Lindström, & P. Widén. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia--occurrence and distribution. Holarct. Ecol. 8:285-298.

Bendell, J. F., D. G. King & D. H. Mossop. 1972. Removal and repopulation of blue grouse in a declining population. J. Wildl. Manage. 36:1153-1165.

Bergerud, A. T. 1987. Reply to Watson and Moss (1987). Can. J. Zool. 65:1048-1050.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pp. 578-685 *in* A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Bergerud, A. T. & H. E. Butler. 1985. Aggressive and spacing behavior of female blue grouse. Auk 102:313-322.

Bergerud, A. T., D. H. Mossop, & S. Myrberget. 1985. A critique of the mechanics of annual changes in ptarmigan numbers. Can. J. Zool. 63:2240-2248.

Bergmann, H.-H., S. Klaus, F. Müller, & J. Wiesner. 1975. Individualität und Artspezifität in den Gesangsstrophen einer Population des Haselhuhns (*Bonasa bonasia bonasia* L., Tetraoninae, Phasianidae). Behaviour 55:94-114.

Bergmann, H.-H., S. Klaus, F. Müller, & J. Wiesner. 1982. Das Haselhuhn, *Bonasa bonasia*, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Boag, D. A. & M. A. Schroeder. 1987. Population fluctuations in spruce grouse: what determines their numbers in spring? Can. J. Zool. 65:2430-2435.

Børset, O. 1985. Skogskjøtsel I, skogøkologi. Landbruksforlaget, Oslo. (In Norwegian)

Brittas, R. & M. Karlbom. 1990. A field evaluation of the Finnish 3-man chain: a method for estimating forest grouse numbers and habitat use. Ornis Fenn. 67:18-23.

Brown, J. L. 1969a. Territorial behavior and population regulation in birds. Wilson Bull. 81:293-329.

Brown, J. L. 1969b. The buffer effect and productivity in tit populations. Am. Nat. 103:347-354.

Brown, J. L. & G. H. Orians. 1970. Spacing patterns in mobile animals. Ann.

Rev. Ecol. Syst. 1:239-263.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Aust. 2:51-78.

Doerr, P. D., L. B. Keith, D. H. Rusch & C. A. Fischer. 1974. Characteristics of winter feeding aggregations of ruffed grouse in Alberta. J. Wildl. Manage. 38:601-615.

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Enoksson, B. 1990. Autumn territories and population regulation in the nuthatch Sitta europaea: an experimental study. J. Anim. Ecol. 59:1047-1062.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, New Jersey.

Fretwell, S. D. & H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:16-36.

Gauthier, G. 1987. The adaptive significance of territorial behaviour in breeding buffleheads: a test of three hypotheses. Anim. Behav. 35:348-360.

Gavrin, V. F. 1969. Ekologiya ryabchika v Belovezhskoi Pushche. Gosudarstvennoe Zapovedno-Okhotnich'e Khozyaistvo "Belovezhskaya Pushcha" 3:146-172. (In Russian)

Gjerde, I. & P. Wegge. 1989. Spacing pattern, habitat use and survival of capercaillie in a fragmented winter habitat. Ornis Scand. 20:219-225.

Gullion, G. W. 1990. Management of aspen for ruffed grouse and other wildlife--an update. Pp. 133-143 in R. D. Adams, ed. Aspen symposium '89. U. S. For. Serv., Gen. Tech. Rep. NC-140.

Hagen, Y. 1952. Rovfuglene og viltpleien. Gyldendal Norsk Forlag, Oslo. (In Norwegian)

Hannon, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alteration of sex ratio. J. Anim. Ecol. 52:807-820.

Hannon, S. J. 1988. Intrinsic mechanisms and population regulation in grouse--a critique. Acta Congr. Intern. Ornithol. 19:2478-2489.

Hannon, S. J., L. G. Sopuck & F. C. Zwickel. 1982. Spring movements of female blue grouse: evidence for socially induced delayed breeding in yearlings. Auk 99:687-694.

Hannon, S. J. & F. C. Zwickel. 1987. Spacing behavior and population regulation in female blue grouse. Auk 104:344-345.

Harvey, M. J. & R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum area method. J. Mammal. 46:398-402.

Herzog, P. W. & D. A. Boag. 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. 42:316-323.

Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115:510-530.

Hixon, M. A. 1987. Territory area as a determinant of mating systems. Am. Zool. 27:229-247.

Hjorth. I. 1976. The divalent origin and adaptive radiation of grouse songs. Ornis Scand. 7:147-157.

Hörnfeldt, B., O. Löfgren, & B.-G. Carlsson. 1986. Cycles in voles and small game in relation to variations in plant production indices in northern Sweden. Oecologia 68:496-502.

Huxley, J. 1934. A natural experiment on the territorial instinct. Brit. Birds 27:270-277.

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In Russian)

Jenkins, D., A. Watson, & G. R. Miller. 1963. Population studies on red grouse, Lagopus lagopus scoticus (Lath.) in north-east Scotland. J. Anim. Ecol. 32:317-376.

Jurgenson, P. B. 1961. A study of fluctuations of populations of the hazel grouse. Proc. Baltic Ornithol. Conf. (Riga) 4:91-96.

Keith, L. B. 1974. Some features of population dynamics in mammals. Proc. Intern. Congr. Game Biol. 11:17-58.

Keith, L. B. & D. H. Rusch. 1988. Predation's role in the cyclic fluctuations of ruffed grouse. Acta Congr. Intern. Ornithol. 19:699-732.

Kenward, R. 1987. Widlife radio tagging; equipment, field techniques and data analysis. Academic Press, London.

Klaus, S., J. Wiesner & R. Bräsecke. 1975. Revierstruktur und Revierverhalten beim Haselhuhn (Tetrastes bonasia L.). Beitr. Jagd- und Wildforsch. 9:443-452.

Klomp, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. Netherl. J. Zool. 22:456-488.

Klyver, H. N. & L. Tinbergen. 1953. Territory and the regulation of density in titmice. Arch. Néerl. Zool. 10:265-286.

Krebs, J. R. & N. B. Davies. 1981. An introduction to behavioural ecology. Sinauer Ass. Inc. Publ., Sunderland, Massachusets.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.

Lance, A. N. 1978. Territories and the food plant of individual red grouse. II. Territory size compared with an index of nutrient supply in heather. J. Anim. Ecol. 47:307-313.

Leclerq, B. 1988. Premières données sur la comparaison de la dynamique des populations de grand tétras (Tetrao urogallus) et de gelinottes des bois (Bonasa bonasia) d'un même massif forestier du Haut-Jura. Gibier Faune Sauvage 5:273-288.

Lindén, H. 1988. Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. Oikos 52:341-349.

Lindén, H. & M. Wikman. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. J. Anim. Ecol. 52:953-968.

Lindström, E., P. Angelstam, P. Widén, & H. Andrén. 1987. Do predators synchronize vole and grouse fluctuations?--an experiment. Oikos 48:121-124.

Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. J. Anim. Ecol. 47:461-475.

Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35:185-193.

Lomnicki, A. 1988. Population ecology of individuals. Univ. Princeton Press, Princeton, New Jersey.

MacLean, S. F., Jr. & T. R. Seastedt. 1979. Avian territoriality: sufficient resources or interference competition. Am. Nat. 114:308-312.

Marcström, V., R. E. Kenward & E. Engren. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. J. Anim. Ecol. 57:859-872.

Martin, K., S. J. Hannon & S. Lord. 1990. Female-female aggression in white-tailed ptarmigan and willow ptarmigan during the pre-incubation period. Wilson Bull. 102:532-536.

Miller, G. R. & A. Watson. 1978. Territories and the food plant of individual red grouse. I. Territory size, number of mates and brood size compared with the abundance, production and diversity of heather. J. Anim. Ecol. 47:293-305.

Moss, R. & I. Hanssen. 1980. Grouse nutrition. Commonwealth Bur. Nutr., Nutr. Abstr. Rev.--Ser. B. 50:555-567.

Moss, R., A. Watson & R. Parr. 1988. Mate choice by hen red grouse Lagopus lagopus with an excess of cocks--role of territory size and food quality. Ibis 130:545-552.

Pedersen, H. C. 1988. Territorial behaviour and breeding numbers in Norwegian willow ptarmigan: a removal experiment. Ornis Scand.19:81-87.

Potapov, R. L. 1985. Fauna SSSR, ptitsy, otryad kyroobraznye (Galliformes), semeistvo teterevinye (Tetraonidae). Nauka, Leningrad. (In Russian)

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Scherzinger, W. 1981. Stimminventar und Fortpflanzungsverhalten des Haselhuhnes Bonasa bonasia. Ornithol. Beob. 78:57-86.

Scherzinger, W. 1982. Trials with natural broods of grouse. Proc. Intern. Symp. Grouse 2:199-201.

Schoener, T. W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. Am. Zool. 27:259-291.

Semenov-Tyan-Shanskii, O. 1959. Ekologiya teterevinykh ptits. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1-318. (In Russian)

Stamps, J. A. & K. Tollestrup. 1984. Prospective resource defense in a territorial species. Am. Nat. 123:99-114.

Steen, J. B., H. Steen, N. C. Stenseth, S. Myrberget, & V. Marcström. 1988. Microtine density and weather as predictors of chick production in willow ptarmigan, Lagopus l. lagopus. Oikos 51:367-373.

Stenman, O. & M. Helminen. 1974. Aging method for hazel grouse (Tetrastes bonasia) based on wings. Suomen Riista 25:90-96. (In Finnish, English summ.)

Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse Bonasa bonasia in spring and autumn. Ornis Fenn. 68:in press.

Swenson, J. E. In press. Is the hazel grouse a poor disperser? Trans. Congr. Int. Union Game Biol. 20:

Szuba, K. J. & J. F. Bendell. 1988. Nonterritorial males in populations of spruce grouse. Condor 90:492-496.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Watson, A. 1965. A population study of ptarmigan (Lagopus mutus) in Scotland. J. Anim. Ecol. 34:135-170.

Watson, A. 1985. Social class, socially-induced loss, recruitment and breeding of red grouse. Oecologia 67:493-498.

Watson, A. & D. Jenkins. 1964. Notes on the behaviour of the red grouse. British Birds 57:137-170.

Watson, A. & D. Jenkins. 1968. Experiments on population control by territorial behaviour in red grouse. J. Anim. Ecol. 37:595-614.

Watson, A. & R. Moss. 1979. Population cycles in the Tetraonidae. Ornis Fenn. 56:87-109.

Watson, A. & R. Moss. 1987. The mechanics of annual changes in ptarmigan numbers: a reply to Bergerud, Mossop, and Myrberget. Can. J. Zool. 65:1043-1047.

Watson, A. & R. Moss. 1988. Spacing behavior and population limitation in red grouse. Auk 105:207-208.

Wiley, R. H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49:201-227.

Zbinden, N. 1979. Zur Ökologie des Haselhuhns Bonasa bonasia in den Buchenwäldern des Chasseral, Faltenjura. Ornithol. Beob. 76:169-214.

Zwickel, F. C. 1972. Removal and repopulation of blue grouse in an increasing population. J. Wildl. Manage. 36:1141-1152.

Zwickel, F. C. 1980. Surplus yearlings and the regulation of breeding density in blue grouse. Can. J. Zool. 58:896-905.

V. RELATIONSHIPS BETWEEN MALE AND FEMALE HAZEL GROUSE DURING THE NONBREEDING SEASON

INTRODUCTION

During the nonbreeding season, birds show a wide range of social organizations, from solitary individuals that aggressively defend feeding territories to flocks that show no territorial boundaries (Pulliam & Millikan 1982). Even among nonsolitary territorial species, there is a wide range of social relationships. For example, tree creepers (Certhia familiaris) defend exclusive territories but rely on other members of the "pariform guild" to provide vigilance against predators while foraging (Hogstad 1990) and dominant pied wagtails (Motacilla alba) allow satellite wagtails to share and help defend the territory when food is readily available (Davies & Houston 1983). Nuthatches (Sitta europaea) defend territories as pairs (Löhrl 1958) and most tits in temperate regions associate in discrete, nonkin flocks that defend a common territory and provide each other with vigilance against predators (Ekman 1989).

Territoriality is a response to ecological requisites that are in short supply, yet are economically defensible (Brown 1964). Ecological variables impose limits on the types of social organization that will be adaptive. Thus, social organization should be a response to ecological constraints, determined by the relative costs and benefits to individuals of different forms of social organization (Gosling & Petrie 1981, Pulliam & Millikan 1982). Two of the obvious costs of coinhabiting a territory are sharing the limited resource that is defended against conspecifics and defending a territory twice as large as required for only one bird. Potential benefits of sharing a territory include help with defense, help in locating food, increased vigilance against predators, and the ability to exploit food resources farther from cover (Orians 1971, Pulliam & Millikan 1982, Elgar 1986, Ekman 1989).

The hazel grouse (Bonasa bonasia) of Palearctic boreal and montane forests is territorial during the nonbreeding season (except summer) (Chapter IV). It is well known that males and females are often seen together during the nonbreeding season, but it is not known if male and female territories coincide or even if these grouse are actually "pairs", since no studies have involved marked birds (Pynnönen 1954, Bergmann et al. 1982). Hazel grouse, however, have often been reported to form pair bonds in autumn and live monogamously throughout the year (Donaurov 1947, Dement'ev et al. 1967, Hjorth 1970, Glutz 1973, Aschenbrenner 1985).

In this study, my objectives were to document the relationship between male and female hazel grouse during the nonbreeding season, and to examine the possible benefits of sharing a territory by asking three questions: 1) do both birds defend a common territory to share the cost of defense and increase its effectiveness (Davies & Houston 1983, Enoksson 1987), as hazel grouse habitats are in dense forest, and intrusion into a hazel grouse territory by neighbors varies linearly with territory size (Chapter IV)? 2) do two birds increase vigilance for predators enough to allow an increased foraging rate (Caraco 1979, Pulliam & Millikan 1982, Huempfner & Tester 1988, Ekman

1989, Hogstad 1990)? and (3) are two birds able to forage farther from cover than singles (Elgar 1986)?

STUDY AREA AND METHODS

The study area (285 ha, of which 195 ha was forest) was within a forest reserve on the Grimsö Wildlife Research Area in southcentral Sweden (59-60° N and 15-16° E). It is described in detail in Chapter VII.

Hazel grouse were captured and outfitted with necklace-mounted radio transmitters and located four to six times per week by triangulation from June 1987 to June 1990. Territory sizes were determined by the modified minimum area method (Harvey & Barbour 1965) when ≥25 locations were obtained in a season. Seasons were defined a priori as spring (April-May), summer (June-August), autumn (September-October), and winter (November-March), based on a behavioral study at a similar latitude in Finland (Pynnönen 1954). "Pairs" were defined as a male and female, both radio-marked, whose territories overlapped more with each other than with other grouse. All observations of members of a pair with other grouse were recorded.

Whether the territories of a pair coincided spatially was tested by calculating the amount of territory overlap for each pair, expressed as the mean amount of the overlap, in percent, of each bird's territory. Territories were considered to coincide spatially during a given season if the 95% confidence interval for these means included 100% overlap. Pairs were considered to be together when located simultaneously ≤20 m apart (74% of determined locations were within 20 m of true locations, Chapter IV). The members of a pair were considered to comprise a social unit if they were located together more than expected. The expected value was determined from the distances between 200 random pairs of points within a square the same size as the mean territory size for that season (data in Chapter IV).

In winter, grouse suspected to be foraging were approached as unobtrusively as possible in an attempt to obtain data on foraging rates. Additionally, the species of tree, height of tree, position of bird in the tree crown (by thirds), and distance of the tree from continuous spruce forest were recorded. Deciduous trees were considered to be outside spruce forest if they were found in an opening (usually a fen) exceeding 10 x 40 m in size. Birds were considered to be foraging together if they could see each other. Although the spruce forest was dense, I feel that few second birds were missed because, when together, they almost always foraged in the same or adjacent trees (based on radio-marked birds), they flapped audibly as they foraged (0.4-0.5 times per min, heard up to 70 m away), and could be heard easily as they flushed from the trees. Foraging rate was the time required to ingest 20 bites. Time spent loafing, with the body down against the branch and neck withdrawn, was excluded. Vigilance could not be distinguished from searching for buds and catkins; if more time were spent taking 20 bites, it was assumed to indicate an increase in the time spent on vigilance. To avoid dependence of the data, the mean time to ingest 20 bites during a foraging bout for each bird was used in statistical tests. A foraging bout is the period that foraging was observed for a given bird in a given tree.

Data on the distances of alder from continuous spruce cover were from a census of the entire study area described in Chapter VII. Only alders ≥10 m tall were included, because they were highy preferred for foraging by hazel grouse (Chapter VII). The Chi-square goodness-of-fit test and the Bonferroni family of simultaneous confidence intervals were used to test use of alders at various distances from spruce forest relative to availability (Neu et al. 1974). Whenever a 2x2 contingency test was used, it was corrected for continuity with Yate's correction. Throughout, means are presented with the standard error of the mean.

RESULTS

Territorial overlap and spatial relationships between males and females

Territories of males and females often overlapped extensively, and the placement of territories suggested that at least some males and females were associated as social units (Fig. V-1). The mean overlap of the territories of a pair was 65% (95% C.I.=33-97%, N=6) in summer, 65% (38-91%, N=6) in autumn, and 53% (0-129%, N=4) in winter. There was no significant difference among seasons (Kruskal-Wallis test, H=1.21, df=2, P>0.50). The overlap in winter was based on a small sample size with high variance. Combining autumn and winter data, and using the greater value when data were available for a pair during both autumn and winter, resulted in a mean of 67% (39-95%, N=7). Thus, although they overlapped a good deal, it appeared that males and females in a pair did not defend the same space during the nonbreeding season, because 100% overlap was outside the 95% confidence interval. This contrasted with the situation in the spring, when pairs did defend, by this definition, common territories (Chapter II).

Members of a pair were together more than was expected by chance. In summer, they were located ≤20 m apart during 19±6% of the relocations (N=6 pairs). Males appeared to be with broodless hens more (28±4%, N=4) than with hens with broods (1±1%, N=2). In autumn, they were together 24±7% (N=6) of the time, and in winter, 19±4% (N=5). These percentages contrast with those of 200 random pairs of positions within average-sized territories that were ≤20 m apart: 0.5% in summer, 1.5% in autumn, and 0.5% in winter. Thus, the pairs were together more than expected during each season (P=0.047 in summer, P=0.03 in autumn, and P=0.043 in winter, Wilcoxon signed rank tests). The summer data for females with and without broods were combined for this test. Although sample sizes were small, males appeared to use the territories independently of females with broods in summer. These tests were conservative, because the random distances were obtained assuming 100% overlap of territories, which was not the case. For comparison, the pairs were together 37±5% of the time in spring, which was also more than expected (Chapter II). There were no significant differences in the amount of time pairs were together during the three nonbreeding seasons (H=2.64, df=3, P>0.10), but they were together more during the breeding season than the nonbreeding

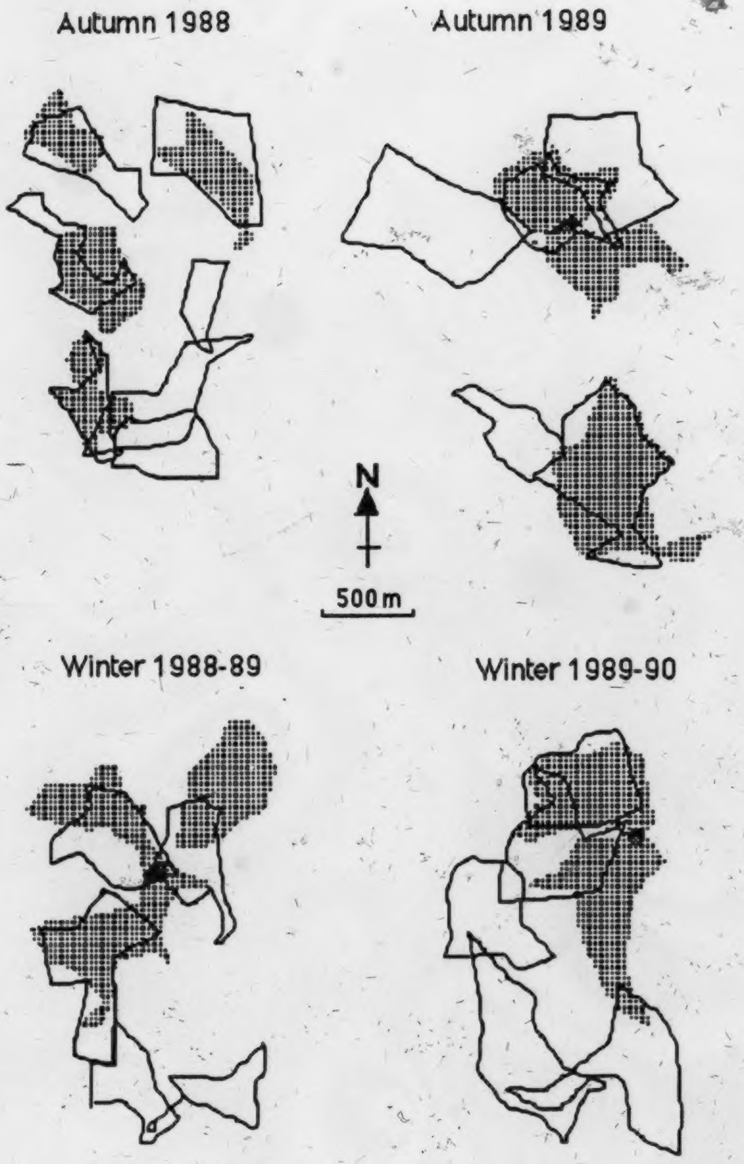

Fig. V-1. Overlap of territories of radio-marked male (lines) and female (shaded) hazel grouse during autumn and winter.

seasons (Mann-Whitney test, U=109, df=24, P=0.02).

Although pairs were together more than expected during the nonbreeding season, the less than complete overlap of the male and female territories suggested that each bird of a pair had the potential to associate with others in neighboring territories. Observations during the territorial period (autumn and winter) revealed that this potential was realized. In autumn, seven males were known to have been with an average of 1.4±0.3 females (1-3) and seven females were with 1.3±0.2 males (1-2, U=25.5, df=13, P=0.87). In winter, six males were with 1.7±0.3 females (1-3) and seven females were with 2.0±0.2 males (1-3, U=27, df= 12, P=0.34). All of the "extra" birds were outside the territory of the other member of the pair. These values are all minimum estimates because not all neighbors were radio-marked and because not all instances when birds were together were recorded. Combining sexes, the hazel grouse were observed associating with more birds in winter (1.8±0.2) than in autumn (1.4±0.2, U=127.5, df=26, P=0.049).

Winter foraging behavior when alone and together

Hazel grouse on the study area showed a very strong preference for foraging in trees of black alder (*Alnus glutinosa*) in winter (Chapter VII). Birds observed foraging arboreally were evenly divided between singles (48%) and twos (52%, N=124). As most foraging occurred in black alder, where the foraging rate was greater than in birch (unpubl. data), only data on foraging rates in black alder were analyzed here.

There was no difference in mean foraging rates between males and females when alone (U=9, df=8, P=1.0) or together (U=67.5, df=20, P=0.22, two-tailed tests, Table V-1). Therefore, sexes were combined to test for differences between group sizes (Table V-1). When in a group of two, hazel grouse foraged 17% faster than when alone (U=136, df=29, one-tailed P=0.03).

Hazel grouse foraged significantly farther from continuous spruce forest when together than when alone (U=2538.5, df=120, one-tailed P<0.0001, Table V-2). Foraging sites away from spruce cover were in fens or along shorelines and were dominated by deciduous trees. The farthest a single hazel grouse was observed from spruce forest was 9 m, but 98% of the observations were within 6 m. Two grouse were observed foraging together a maximum of 22 m from spruce forest, with 6% of the observations >15 m away. Two birds foraged in somewhat shorter trees than singles (U=2113.5, df=117, two-tailed P=0.04). There was no significant difference in the species of trees ($\underline{X}^2_c$=0.24, df=2, P=0.62) nor in location within the tree crown ($\underline{X}^2$=0.03, df=3, P=0.95, both tests two-tailed).

All hazel grouse combined selected alders that were significantly closer to spruce cover than expected based on availability (Chapter VII). Hazel grouse in both categories foraged in alders in relation to spruce cover differently than expected, based on the distribution of alders on the area (singles, one-group $\underline{X}^2$=34.36, df=3, P<0.0001; pairs, one-group $\underline{X}^2$=34.91, df=3, P<0.0001), but grouse foraging alone selected different categories of alders in relation to their distance from spruce cover than when foraging together (Fig. V-2). Singles

Table V-1. Effects of sex and number of birds on foraging rate (seconds used to take 20 bites) of hazel grouse foraging in black alder in winter.

Group size	Sex		Combined
	Male	Female	
One	47.8±6.3 (6)[a]	44.3±2.1 (3)	46.6±4.1 (9)
Two	38.2±2.6 (13)	39.3±1.6 (8)	38.6±1.7 (21)

[a] Mean in sec±SE (N). Each datum was the mean rate obtained from a foraging bout.

Table V-2. Characteristics of sites used by arboreally foraging hazel grouse when alone or with another bird in winter.

Category	Number of hazel grouse	
	One	Two
Distance to spruce forest, m	2.4±0.3 (56)[a]	6.3±0.7 (65)
Height of tree, m	17.1±0.5 (54)	15.7±0.5 (64)
Species of tree (% alder)	76% (59)	71% (65)
Location in tree crown (% of observations)		
Top third	45% (44)	43% (54)
Middle third	36%	37%
Bottom third	18%	20%

[a] Mean±SE (N).

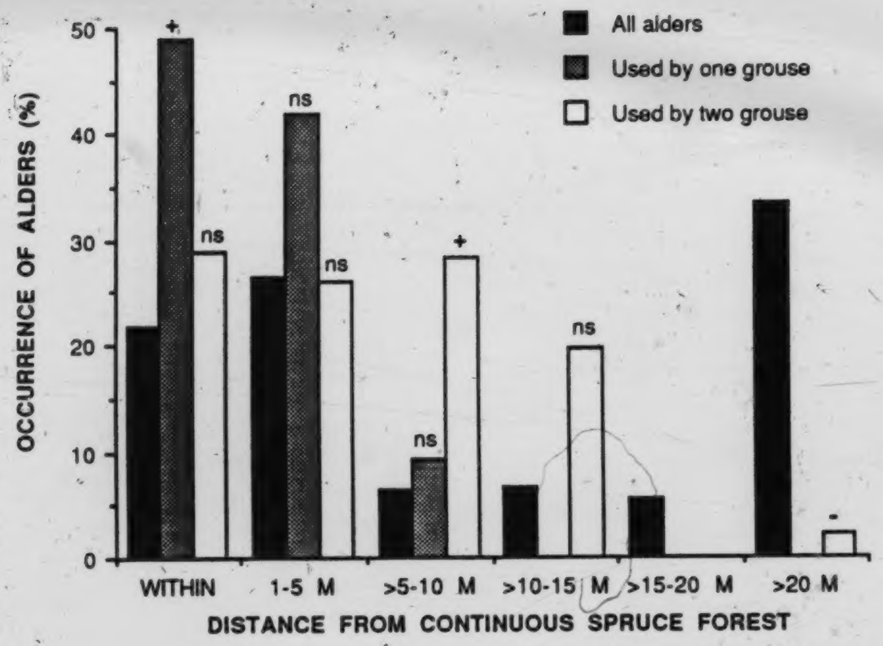

Fig. V-2. Use of alder trees ≥10 m tall by hazel grouse foraging alone and together in relation to distance from continuous spruce forest. A plus indicates use in a category greater than expected based on availability ($P<0.05$), a minus indicates less than expected, and "ns" indicates no difference ($P>0.05$, using the method of Neu et al. 1974)

selected alders surrounded by spruce forest, using them more than expected based on availability. The use of alders 1-10 m from spruce cover was not significantly different from expected, but there was a tendency to use alders 1-5 m from spruce cover more than expected ($P=0.10$). When together, grouse used alders within spruce forest and up to 5 m away as much as expected, and selected alders 5-10 m from spruce cover. The category 10-15 m from spruce cover also received considerable use, although it was not statistically significant. Hazel grouse prefer to forage in trees ≥10 m tall (Chapter VII). The categories used the most by single grouse in relation to their occurrence (0-5 m from spruce forest) contained 48% of the alder trees ≥10 m tall on the study area; whereas those used most in relation to their occurrence by grouse foraging together (5-15 m from spruce forest) contained 13% of these preferred alders (Fig. V-2). Thus, by foraging together, hazel grouse had access to about 27% more food trees on the study area than if they had only foraged alone.

DISCUSSION

During the nonbreeding season, males and females, the territories of which overlap, form a social unit, as they are together much more than expected by chance. However, their territories do not coincide spatially and both sexes spend time with other hazel grouse of the opposite sex, which also share parts of their respective territories. Thus, perhaps a male and female should be considered partners rather than a pair. Hazel grouse were recorded associating with more neighbors in winter than autumn. This may have been an artifact of the greater chance of recording such visits in winter (5 months) than in autumn (2 months). Such a relationship between male and female hazel grouse during the nonbreeding season has not been described previously (Bergmann et al. 1982). Pynnönen (1954) reported that pairs often separated and then reunited during the nonbreeding season. Based on my results, this can be interpreted as one member of the pair spending time with a neighbor within their common space.

The social organization shown by birds can be considered as a compromise between the costs of sharing a resource versus the benefits of being together (Pulliam & Millikan 1982). Three potential benefits of sharing a territory were examined in this study: 1) shared defense of a common territory, 2) protection while foraging together through increased vigilance, and 3) the ability for two birds to forage farther from cover than a single bird. As males and females did not defend a common territory, common defence was not a benefit of shared territories. However, the results showed that two birds did gain benefits from increased foraging rates (suggesting lowered vigilance rates) and from the ability to forage farther from cover than single birds. An apparent cost for a hazel grouse sharing its territory with another is that it would have to defend a territory with twice as much winter food, an apparently important limiting resource (Chapter VII). This was actually not the case, however, because birds foraged much farther from spruce cover when together than when alone. Therefore, about 27% more alders probably were available to two birds than one, partially mitigating the cost of defending a larger territory. Alder trees that grow away from spruce forest also may be more valuable food trees, containing more catkins and buds than those in the spruce forest that compete with spruce for light and nutrients.

An important advantage of overwintering together appeared to be protection from predators. Winter was a period of relatively high mortality during this study (Chapter VIII). Moreover, hazel grouse foraging in bare deciduous trees are probably vulnerable to attack by avian predators. Goshawks (Accipiter gentilis), the most important hazel grouse predator on the study area (Chapter VIII), hunt on the study area by ambush, remaining concealed while searching for prey for about 3 min before flying to another site (Widén 1984). Not only are hazel grouse visible while foraging in bare deciduous trees, but they also can draw attention to themselves when they move (about 2.4 times per min) and flap their wings (about once per minute). About 43% (N=84) of these wing flaps are audible (up to 70 m away). Hazel grouse use thick spruce cover as protection from predators (Donaurov 1947, Scherzinger 1979), so, when foraging away from spruce cover, they are not only farther from protective cover, but they have to fly over an open area, usually towards the predator (goshawk), to reach it. It is well documented that goshawks attack and kill hazel grouse while they are foraging arboreally (Donaurov 1947, Pynnönen 1954, Semenov-Tian-Shanskii 1959, Gavrin 1969, Chapter VI). Several studies have documented that a single bird detects predators less effectively than several and that lone birds forage more slowly than several, presumably because they must spend more time watching for predators (Caraco 1979, Pulliam & Millikan 1982, Elgar 1986, Huempfner & Tester 1988, Ekman 1989, Metcalfe 1989, Hogstad 1990). By foraging together, besides increasing vigilance for predators, two hazel grouse can forage about 17% faster than a single bird and thus spend less time exposed to predators in the open deciduous trees.

If it was beneficial to forage together, why did birds in trees forage alone about half of the time? Degree of sociality differed with distance from cover, as also found by Metcalfe (1984) and Elgar (1986). Spruce forest serves as concealing cover for both the hazel grouse and its main predator, the goshawk. Thus, whereas it may be important to have two birds present for vigilance when foraging away from spruce cover (selected by birds foraging together), such a benefit may be less important at a foraging site with much cover (selected by singles). Moreover, it may be more dangerous to forage together within spruce cover, because two birds would make more noise (wing flapping) than one, increasing the chance of attracting a predator to a site where its presence would be more difficult to detect by the grouse.

The social organization of hazel grouse in the nonbreeding season, with intrasexual, but not intersexual, territoriality (Chapter IV), insures that the maximum flock size will be two. In fact, groups larger than two are very rare in dense coniferous habitats (Chapter VI). A maximum flock size of two may be most adaptive in thick spruce forests because, although larger groups provide more vigilance, they also may be more detectable by predators in closed habitats (Gosling & Petrie 1981) and require more food. Moreover, the greatest incremental increase in individual foraging rate occurs between a group size of one and two (Caraco 1979, Huempfner & Tester 1988, Metcalfe 1989). Thus, the occurrence of a loose pair relationship during the nonbreeding season may be an adaptation to surviving in a heterogenious habitat, with some of the winter food located in dense cover and some located in more open and dangerous situations.

LITERATURE CITED

Aschenbrenner, H. 1985. Raufüßhühner: Lebensweise, Zucht, Krankheiten, Ausbürgerung. Verlap M. & H. Schaper, Hannover, BRD.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn, Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Caraco, T. 1979. Time budgeting and group size: a test of theory. Ecology 60:618-627.

Davies, N. B. & A. I. Houston. 1983. Time allocation between territories and flocks and owner-satellite conflict in foraging pied wagtails, Motacilla alba. J. Anim. Ecol. 52:621-634.

Dement'ev, G. P., N. A. Gladkov, Yu. A. Isakov, N. N. Kartashev, S. V. Kirikov, A. V. Mikheev & E. S. Ptushenko. 1967. Birds of the Soviet Union, Vol. IV. U.S. Dept. Interior & Nat. Sci. Found., Washington, D.C.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika 4:77-122. (In Russian)

Ekman, J. 1989. Ecology of non-breeding social systems of Parus. Wilson Bull. 101:263-288.

Elgar, M. A. 1986. The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. Behav. Ecol. Sociobiol. 19:433-438.

Enoksson, B. 1987. Local movements in the nuthatch Sitta europaea. Acta Reg. Soc. Sci. Lit. Gothoburgensis, Zool. 14:36-47.

Gavrin, V. F. 1969. Ekologiya ryabchika v Belovezhskoi Pushche. Gosudarstvennoe Zapovedno-Okhotnich'e Khozyaistvo "Belovezhskaya Pushcha" 3:146-172. (In Russian)

Glutz von Blotzheim, U. N., K. M. Bauer & E. Bezzel. 1973. Handbuch der

Vögel Mitteleuropas. Band 5, Galliformes und Gruiformes. Akademische Verlagsgesellschaft, Frankfurt am Main.

Gosling, L. M. & M. Petrie. 1981. The economics of social organization. Pp. 315-382 in C. R. Townsend & P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Harvey, M. J. & R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum area method. J. Mammal. 46:398-402.

Hjorth, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7:183-596.

Hogstad, O. 1990. Winter territoriality and the advantages of social foraging in the treecreeper Certhia familiaris. Fauna norv. Ser. C, Cinclus 13:57-64.

Huempfner, R. A. & J. R. Tester. 1988. Winter arboreal feeding behavior of ruffed grouse in east-central Minnesota. Pp 122-157 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Löhrl, H. 1958. Das Verhalten des Kleibers. Z. Tierpsychol. 15:191-252.

Metcalfe, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? Anim. Behav. 32:981-985.

Metcalfe, N. B. 1989. Flocking preferences in relation to vigilance benefits and aggression cost in mixed-species shorebird flocks. Oikos 56:91-98.

Neu, C. W., C. R. Byers & J. M. Peek. 1974. A technique for analysis of utilization--avalability data. J. Wildl. Manage. 38:541-545.

Orians, G. 1971. Ecological aspects of behavior. Avian Biol. 1:513-546.

Pulliam, H. R. & G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biol. 6:169-197.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Scherzinger, W. 1979. Zum Feindverhalten des Haselhuhnes (Bonasa bonasia). Vogelwelt 100:205-217.

Semenov-Tian-Shanskii, O. 1959. Ekologiya teterevinykh ptits. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1-318. (In Russian)

Widén, P. 1984. Activity patterns and time-budget in goshawk Accipiter gentilis in a boreal forest area in Sweden. Ornis Fenn. 61:109-112.

VI. FACTORS SHAPING WINTER SOCIAL ORGANIZATION IN HAZEL GROUSE: A COMPARATIVE STUDY IN THE EASTERN AND WESTERN PALEARCTIC

INTRODUCTION

The social organization of a species is in part an adaptation to prevailing environmental conditions and, in many aspects, usually can be understood using only a limited set of environmental variables (Emlen & Oring 1977, Marzluff & Balda 1988). During the nonbreeding season, birds show a wide range of social organization, varying from solitary birds defending territories to flocks without territorial boundaries (Pulliam & Millikan 1982). The spacing behavior of a species in an area is probably a compromise molded by conflicting selective pressures (Davies 1978).

There is wide agreement that the major selective pressures shaping social organization of birds during the nonbreeding season are 1) predation and 2) the abundance and dispersion of food (Orians 1971, Moriarty 1976, Wiens 1976, Bertram 1978, Davies 1978, Pulliam & Millikan 1982, Clark & Mangel 1986, Marzluff & Balda 1988), although they are not mutually exclusive (Krebs & Barnard 1980). The predation hypothesis states that birds in a flock can detect a predator sooner than a single bird and, as a consequence, each bird can spend more time foraging and less time alert (Moriarty 1976, Caraco 1979, Pulliam & Millikan 1982, Wiens 1976, Elgar 1986, Huempfner & Tester 1988, Metcalfe 1989). However, this benefit may vary with the openness of the habitat. Gosling & Petrie (1981) argued that flocking should be more important in open habitats because it is more difficult to detect approaching predators in closed habitats and large groups can be more easily detected by a predator than small groups in closed habitats. The food dispersion hypothesis states that where food resources are plentiful, predictable and dispersed, animals are also dispersed because the resources are defendable; where food resources are less plentiful, patchily distributed and unpredictable, groups are formed because the food is less defendable (because of competition) and members of a given group benefit by sharing information (Brown & Orians 1970, Orians 1971, Wiens 1976, Davies 1978, Pulliam & Millikan 1982, Clark & Mangel 1986). Of course, there are other combinations of food patchiness and abundance, but these are not considered here.

Grouse, members of the subfamily Tetraoninae, show a wide range in types of social organization during the nonbreeding season. Hines (1986) and Bergerud & Gratson (1988) have postulated that flocking may be an antipredator response used by grouse in open areas, because North American forest grouse tend to winter solitarily or in small flocks and grouse in open habitats form large winter flocks. However, assessments of the relative merits of flocking for maximizing feeding or avoiding predators are needed to resolve this issue (Hines 1986). For these types of questions, it is best to study species that exhibit plasticity in their social organization (Brown & Orians 1970). The hazel grouse (Bonasa bonasia), a Palearctic forest grouse that eats the catkins and buds of deciduous trees in winter, is such a species. In Europe, hazel grouse are territorial and overwinter as singles or pairs, whereas in eastern Asia they are reported to overwinter in flocks (Bergmann et al. 1982, Potapov 1989), although there are also a few reports of larger winter groups in European Russia (Potapov 1989). Comparison of foraging rates and foraging sites of hazel grouse foraging alone or in twos in southcentral Sweden suggested that protection from predation was an important reason for two birds to forage together at more open sites (Chapter V). The objective of this study was to compare the winter group sizes and habitats at study sites in the eastern and western Palearctic to determine which hypothesis, predation or food dispersion, provided the better explanation for the differences in winter social organization.

Based on the above review, the predation hypothesis predicts that hazel grouse would form flocks where they foraged in open forests and, at the other end of the spectrum, occur as singles/pairs in dense forest. The food dispersion hypothesis predicts that flocks would form where food was more patchily distributed and less abundant, whereas singles/pairs would occur where food was more evenly dispersed and abundant. In this paper, "pairs" refers to a male and female hazel grouse foraging together in winter. A pair bond is not implied. Throughout this paper, "we" refers to A. V. Andreev and me, who collaborated on this research.

STUDY AREAS

Our study areas were located near the eastern and western edges of the distribution of hazel grouse. In the eastern Palearctic, we had three study areas in northeastern Siberia, all untouched by forestry, or virtually so. Two were on major rivers: midway along the Omolon River, 900 km NE of Magadan (66° 0' N, 159° 2' E, elevation 200 m), and 30 km upstream from the mouth of the Yana River, 100 km WNW of Magadan (59° 55' N, 149° 16' E, elevation 40 m). In most of northeastern Siberia, larch (*Larix cajanderi*) is the only tree species capable of forming forests under the extremely cold conditions (Kuusela 1990). On river islands and other sites directly influenced by the major rivers, there are riparian forests consisting almost entirely of deciduous trees. Major trees at the Omolon River site were *Alnus fruticosa*, *Salix schwerinii*, *S. rorida*, *Populus suaveolens*, *Chosenia arbutifolia*, and *Betula platyphylla*. The deciduous forest at the Yana River site was similar, except that *Salix sakhalinensis* replaced the two other willow species, and *Alnus hirsuta* and *Padus asiatica* were also present. At both sites, there was an ecotonal belt between the riparian deciduous forest and the surrounding larch forest. Depending on the productivity of the site and height above the river, it was 0-200 m wide and was dominated by larch and *Betula platyphylla*.

The third site was near timberline on the south slope of Dukcha Mountain (summit 1024 m), 25 km NW of Magadan (59° 40' N, 151° 36' E), at an elevation of about 400 m. Near timberline on the south slopes of many mountains near the coast of the Sea of Okhotsk, such as Dukcha Mountain, there is an ecotonal mixed forest of larch, *Betula ermanii*, and *Alnus fruticosa*, with an understory of *Pinus pumila* between the subalpine birch belt and the larch forest. This understory is totally covered by snow during the winter. In northeastern Siberia, hazel grouse winter habitat is limited to the riparian deciduous forests, the larch-birch zone of the riparian-larch ecotone, the larch-birch ecotone between the larch forest and the subalpine birch belt on south slopes, and in alder (*Alnus fruticosa*) thickets along streams near timberline. Virtually no hazel grouse occur in the extensive larch forests that dominate the region and form virtually single-species stands.

The one study site in the western Palearctic was a forest reserve, protected from forestry for almost 20 years, in southcentral Sweden at the Grimsö Wildlife Research Area, 40 km N of Örebro (15° 27' N, 59° 38' E, elevation 90 m). The forest was dominated by spruce (*Picea abies*, 56% of trees), Scots pine (*Pinus sylvestris*, 15%), and birches (*Betula pubescens* and *B. pendula*, 23%). Other deciduous trees included *Populus tremula*, *Alnus glutinosa*, *A. incana*, *Salix caprea*, *Sorbus aucuparia*, and *Prunus padus*. In the western Palearctic, hazel grouse habitats are typically spruce-dominated forests with a high deciduous component (Bergmann et al. 1982).

In all study areas, the most important potential predator of the hazel grouse was the goshawk (*Accipiter gentilis*); the red fox (*Vulpes vulpes*) was also present. Other potential predators in the Siberian areas were the eagle owl (*Bubo bubo*), the Ural owl (*Strix uralensis*), the great gray owl (*S. nebulosa*), and the hawk owl (*Surnia ulula*). Gyrfalcons (*Falco rusticolus*) were present, but uncommon, in the Omolon Valley. The sable (*Martes zibellina*) was present in the Siberian areas with larch and *Pinus pumila* present, but rarely ventured into the riparian deciduous forest in winter (based on the occurrence of tracks). The pine marten (*Martes martes*) was common in the Swedish area, but the eagle owl and Ural owl were rare.

Observations were gathered over several winters in most areas; 1972-73 through 1975-76 in Omolon Valley, 1988-89 in Yana Valley, 1983-84 through 1988-89 on Dukcha Mountain, and 1987-88 through 1989-90 at Grimsö.

METHODS

We recorded group size during winter (1 November-31 March) whenever hazel grouse were encountered. Additional data on group size in the area surrounding the Swedish study site came from weekly wildlife observations recorded from the Grimsö Wildlife Research Area (1977-78 through 1989-90), and from the Västmanland Ornithological Society (1980-81 through 1984-85). Whenever possible, sex of the birds was determined from the color of the chin patch. In Siberia, we recorded whether the birds were observed in riparian forest or larch-birch forests (ecotones along the riparian forests and subalpine forests). At arboreal foraging sites, we estimated the cover provided by the tree canopies by looking through a tube (35 mm inside diameter, 100 mm long, with cross-hairs) held vertically from eight points located 5 and 10 m from the foraging tree in the four cardinal directions. At each point, cover (the amount of the sky that was covered) was estimated to the nearest one-eighth of the observation circle. For example, a score of 3 indicated that 2/8-3/8 of the circle was covered. The cover estimates from all points were summed, giving a cover score that could range from 0 (no cover) to 64 (7/8-8/8 cover at all points). The same observer estimated cover in all areas where this variable was measured.

The abundance and dispersion of trees was determined in all study areas except the Omolon Valley. We counted the number of trees ≥3 m tall, by species, within circular plots 10 m in radius located systematically at a density of two per ha. In the Yana Valley, about 30 plots were centered around each foraging site or sites, if close together, at the Dukcha Mountain site an entire 27-ha patch of larch-birch-alder forest was censused, and in Sweden plots were located within the winter territories of five neighboring, radio-marked male hazel grouse.

Data on food habits and age ratios were based on 79 hazel grouse, collected by shooting throughout the 1988-89 winter in the Yana Valley. Age of birds was determined by the amount of spotting on primary IX (Gaidar & Zhitkov 1974). A logistic regression was used to test for changes in the proportion of adults and juveniles over time (Hosmer & Lemeshow 1989). Tree species used for food were determined from crop contents (Omolon and Yana valleys) or foraging observations (Sweden). Preferred species were those used significantly ($P<0.05$) more than expected based on their availability, following the method of Neu et al. (1974). Important species were those that comprised more than 5% of the diet.

Throughout this paper, we refer to two groups of trees: conifers and deciduous trees. Conifers include three genera of the Family Pinaceae (*Pinus*, *Picea*, *Larix*). Deciduous trees include members of the families Salicaciae, Betulaceae, and Rosaceae. Means are presented with the standard error of the mean. When frequency data were tested using a 2x2 contingency test, the results were corrected for continuity with Yate's correction.

RESULTS

Size and Composition of Winter Groups

Nowhere did we find a correlation between winter group size and week of observation (Yana Valley, $r_s= -0.024$, df=35, $P=0.89$; Omolon Valley, $r_s= -0.032$, df=66, $P=0.82$; Sweden, $r_s=0.018$, df=329, $P=0.75$, Spearman rank correlations). Therefore, in the following analyses, we combined group size from the entire winter period.

Group sizes in northeastern Siberia varied according to habitat (Table VI-1). Here, we excluded observations of roosting grouse in the riverbottom areas, because when there was not enough snow for snow-roosting, groups that had been foraging in the riparian forest often flew intact into the adjacent larch-birch forest to roost in larch trees. Thus, the data included observations of grouse that were foraging or loafing above the snow. Groups were larger in deciduous riparian forests than in the ecotonal larch-birch forests in both the Yana Valley (Mann-Whitney test, U=110.5, df=29, $P=0.04$) and the Omolon Valley (U=581, df=68, $P=0.0001$), but did not vary significantly in size between areas in riparian forests (U=749.5, df=80, $P=0.44$) nor among three areas in larch-birch forests (Kruskal-Wallis test, H=1.302, df=2, $P>0.50$). The combined data showed that group size in deciduous forests averaged more than three

Table VI-1. Sizes of winter groups of hazel grouse in Siberia and Sweden in different forest types.

	Forest type		
Area	Riparian (Deciduous)	Ectone (Larch-birch)	Coniferous (Spruce)
Yana Valley	9.0±1.9 (24)[a]	2.5±1.0 (6)	
Omolon Valley	5.1±0.4 (57)	2.0±0.2 (12)	
Dukcha Mountain		1.7±0.3 (10)	
Grimsö			1.4±0.03 (331)
Combined	6.3±0.6 (81)	2.0±0.2 (28)	1.4±0.03 (331)

[a] Mean±SE (N).

times greater than those in larch-birch forests, a highly significant difference (U=1856, df=108, P<0.0001).

The age ratio of shot grouse did not vary by habitat type. Within the riparian forests of the Yana Valley, 27% of 56 hazel grouse collected during October 1988 to March 1989 were juveniles, compared to 14% of 7 in the adjacent larch-birch forest, a nonsignificant difference ($\underline{X}^2_c$=0.06, df=1, P=0.80). However, the proportion of juveniles among collected grouse declined significantly over the winter (maximum likelihood ratio test, G=9.74, df=1, P<0.005, Fig. VI-1).

Winter group sizes at Grimsö were very small, averaging only 1.4 birds (Table VI-1). This was significantly smaller than those in the Siberian riparian forests combined (U=23735.5, df=411, P<0.0001) and larch-birch forests combined (U=5904.5, df=358, P=0.005).

Winter groups in Siberia were not segregated sexually. When we had the opportunity to identify their sexes, we found that 82% of lone birds were males (N=11), 53% of birds in pairs were males (N=32), and 55% of birds in groups of three or more were males (N=77). Of the 15 groups greater than three in which we could determine the sex of at least two birds, 13 (87%) were mixed, containing both sexes. Overall, 68 of 120 birds identified to sex were males (57%).

In Sweden, groups of two birds were almost always one male and one female. Of 42 instances when both birds could be identified to sex, 41 were one male and one female (98%). Only once were both of the same sex (males, one radio-marked, observed in the same tree on the border between their territories). The composition of only one group greater than two was determined; a group of three (all unmarked) contained one male and two females.

Behavior of Birds in Groups

Although grouse in the Siberian study areas were not radio-marked, it was our impression that the groups were relatively stable assemblages of birds, particularly the smaller groups. We observed several behaviors that suggested that such groups were maintained. For example, after a group was dispersed by human disturbance, they would begin to sing within 10-15 min and then regroup (S. Drovetskii, pers. comm.). They also would sing after emerging from snow roosts, perhaps to reunite the group before foraging. Groups also appeared to stop foraging and to enter snow roosts at the same time, often roosting within a few meters of one another. When snow conditions were not conducive to snow roosting in the riparian forest, because the snow was too shallow or wet, the grouse would fly as a group into the nearby larch-birch forests to roost there. Thus, singing in this context appeared to maintain contact with other members of the group. Hazel grouse answered an imitation of the song in autumn in Siberia, but only approached or acted aggressively early in that season. By late September, aggressive responses to the imitations had subsided. In spring, males approached and acted aggressively to an imitation

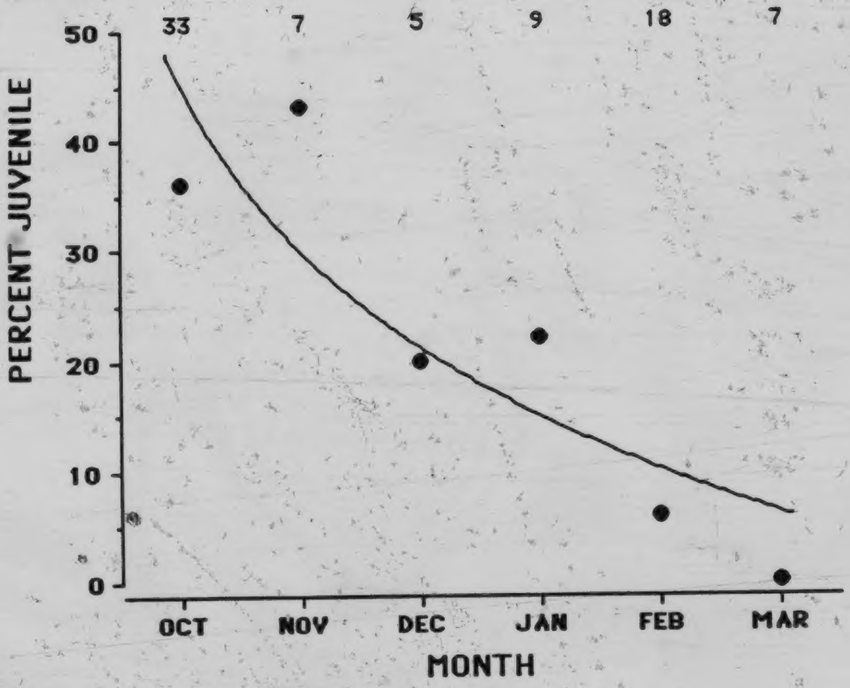

Fig. VI-1. Percentage of juvenile hazel grouse in monthly samples of hazel grouse collected in Yana Valley, Siberia during the 1988-89 winter. Numbers at the top of the graph are sample sizes of shot birds (logistic regression, maximum likelihood ratio test, G=9.74, df=1, P<0.005).

of the song and only then did we hear flutter jumps and flutter flights.

We have one observation of behavior of a group of hazel grouse during a predator attack. At 1200 on 14 March 1974 in the Omolon Valley, A. V. Andreev observed 13 hazel grouse (5 males and 8 females) foraging in the crown of a Chosenia arbutifolia tree. Suddenly, the group "exploded" in all directions, and immediately afterwards a goshawk swooped into the empty tree, but it failed to catch any grouse. Andreev found one of the males hiding alone in a small tree under a cap of snow. He was able to approach it closely enough to touch it. It then flew down to the snow and dug into it, covering itself completely.

In Sweden, behavior was very different than in Siberia. Hazel grouse in winter were clearly territorial against other members of the same sex (Chapter IV). Territoriality was advertised with songs, flutter jumps and flutter flights that were heard in both autumn and spring. Males reacted aggressively to an imitation of the song in both seasons (Swenson 1991, Chapters II & IV). However, when a pair was disturbed and the birds became separated, they would also often sing until they were reunited.

Cover at Foraging Sites

In winter, arboreally foraging hazel grouse were readily observable to visual predators, especially in deciduous forests, as they moved about in the bare trees. In the riparian forests of the Omolon Valley, Andreev was able to discover them foraging from a distance of ca. 250 m. When hazel grouse lost their balance on branches or flew to another branch, they flapped their wings audibly. In the dense spruce forests at Grimsö, Swenson has heard this sound up to 70 m away, and in the open deciduous forests of the Omolon Valley, Andreev heard it at ca. 250 m away (at ca. -45° C). Thus, hazel grouse are potentially vulnerable to being discovered and attacked by avian predators while foraging arboreally.

The amount of cover provided by the tree canopy and the number of coniferous and deciduous trees within 10 m of the tree used for foraging varied greatly between the Yana Valley and Grimsö (Table VI-2). The grouse in the Yana Valley, foraging within a deciduous riparian forest, has less cover ($U=1026.5$, $df=120$, $P=0.001$), fewer coniferous trees ($U=1140$, $df=120$, $P<0.0001$), more deciduous trees ($U=1060.5$, $df=120$, $P=0.0006$), and more total trees ($U=940.5$, $df=120$, $P=0.016$) at foraging sites than the Swedish grouse.

Data were not available from feeding sites in larch-birch forests. However, larch-birch forests contain higher densities of larch and appeared to provide hazel grouse with more cover than the deciduous forests because, even though bare of needles, the larch had a higher density of branches, especially fine branches, and a higher density of buds, which were larger and darker than those of deciduous trees. The density of larches was 45% greater in the timberline forest at Dukcha Mountain (153±22/ha) than the combined foraging sites in riparian forest in the Yana Valley (105±16, $U=6852.5$, $df=233$, $P<0.0001$). For comparison along the Yana River, we counted trees on a 20-ha plot on an island within the deciduous forest and on a 26-ha plot in the ecotonal

Table VI-2. Cover and forest density at winter foraging sites of hazel grouse in riparian forest (Yana Valley, Siberia) and spruce forest (Grimsö, Sweden) in relation to group size.

	Spruce forest		Riparian forest
Category [a]	Singles	Pairs	Groups
Cover index	30.9±1.3[b]	21.2±1.0	16.4±1.3
No. coniferous trees	21.4±1.6	13.3±1.4	4.0±2.2
No. deciduous trees	17.9±1.9	30.2±3.1	77.6±16.4
No. total trees	39.3±2.2	43.6±2.5	81.6±15.7
Sample size	50	59	12

[a] All data gathered within a 10-m radius of the tree used for foraging.

[b] Mean±SE.

larch-birch forest across a river channel ca. 30 m away. The trees in the deciduous forest were 15-20 m tall and had diameters at 1.5 m of 15-20 cm; in the larch-birch forest they were 20-25 m tall and 20-30 cm in diameter (with some up to 40 cm). The larch-birch forest site contained 146% more larches (557±41/ha) than the adjacent riparian forest site (226±60, U=1699.5, df=91, $P<0.0001$), but the density of deciduous trees in the riparian forest (1270±124) was almost eight times greater than that in the larch-birch forest (166±35, U=1986, df=91, $P<0.0001$).

At Grimsö, hazel grouse foraging alone used forests with more cover than hazel grouse foraging as a pair (Table VI-2). Single birds used sites that had more cover (U=2307.5, df=108, $P<0.0001$), more coniferous trees (U=2060.5, df=108, P=0.0004), fewer deciduous trees (U=1932.5, df=108, P=0.005), but similar total numbers of trees (U=1681.5, df=108, P=0.21). Based on these results from Sweden, we would expect the Siberian grouse, which forage in groups, to be in even more conspicuous sites than pairs in Sweden. This was the case (Table IV-2). Siberian grouse foraged at sites with less cover (U=461, df=70, P=0.039), fewer coniferous trees (U=566.5, df=70, P=0.0005), and more deciduous trees (U=532, df=70, P=0.003) than Swedish pairs. These tests were one-tailed, because the direction of the results was expected. Foraging sites in the Yana Valley were in denser forest than those of pairs at Grimsö (U=486.5, df=70, P=0.04, two-tailed test).

In the Yana Valley, hazel grouse foraging sites did not differ significantly from the surrounding forest with respect to density of coniferous, deciduous, or total trees (Table VI-3). At Grimsö, however, both pairs and singles foraged at sites with more deciduous trees and fewer coniferous trees than was found within their winter territories. Pairs chose sites with greater overall tree density, whereas there was no statistical difference for singles (Table VI-3).

Distribution and Abundance of Winter Food

Hazel grouse in both the Yana Valley and at Grimsö foraged in deciduous trees (Table VI-4). In the Yana Valley, hazel grouse were documented eating from only four of the eight available deciduous trees; two species were preferred (Betula platyphylla and Chosenia arbutifolia) but all four were important (comprising >5% of the diet). At Grimsö, hazel grouse fed on all the available deciduous trees, but only Alnus spp. was preferred and only Alnus and Betula were important food species. No data on hazel grouse diet was available from Dukcha Mountain, but droppings contained remains of catkins of Betula ermanii and Alnus fruticosa. Because the diet of hazel grouse in the Omolon Valley was similar to that in the Yana Valley (Andreev 1979), we assumed that it was also similar on Dukcha Mountain.

There was a clear difference in the abundance of food trees available to hazel grouse in the three areas (Kruskall-Wallis test, H=135.8, df=2, $P<0.001$ for preferred species and H=205.7, df=2, $P<0.001$ for important species, Table VI-5). Within hazel grouse wintering areas, there was a mean of 204 preferred trees/ha in the riparian forests in the Yana Valley, compared with 344 on Dukcha Mountain but only 44 at Grimsö. All of these were different from each

Table VI-3. Number of trees, by category, within 10 m of sites of hazel grouse foraging in the Yana Valley and at Grimsö in relation to the surrounding forest (> refers to sites with greater tree density than the forest as a whole, and < to sites with less).

	Number of trees (compared to expected)								
	Coniferous			Deciduous			Total		
Area	>	<	P[a]	>	<	P	>	<	P
Yana	8	4	0.41	5	7	0.24	6	6	0.27
Grimsö-pairs	8	15	0.01	18	4	0.002	16	7	0.02
Grimsö-singles	5	13	0.014	12	6	0.01	9	9	0.49

[a] Based on Wilcoxon signed rank test.

Table VI-4. Use of deciduous trees for winter foraging by hazel grouse in the Yana Valley, Siberia, and Grimsö, Sweden.

Area	Tree	Percent on area[a]	Percent of diet[b]	Selection[c]	Category[d]
Yana	*Alnus fruticosa*	63.6	51.1	-	I
	Salix	12.0	13.7	ns	I
	Alnus hirsuta	11.6			
	Populus	6.3			
	Chosenia	4.7	27.2	+	P, I
	Betula	0.9	7.9	+	P, I
	Prunus	0.8			
	Sorbus	0.1			
Grimsö	*Betula*	81.9	23.0	-	I
	Alnus	13.7	74.0	+	P, I
	Populus	2.9	1.7	-	
	Sorbus	1.1	0.3	ns	
	Prunus	0.3	0.3	ns	
	Salix	0.2	0.7	ns	

[a] Of the deciduous trees present.

[b] From dry weights of 55 crops from Yana (Andreev & Drovetskii, in prep.) and 184 foraging observations from Grimsö (Chapter V).

[c] Use compared to expected, + = more ($P<0.05$), - = less ($P<0.05$), ns = no difference ($P>0.05$).

[d] P = preferred (use more than expected), I = important (>5% of diet).

Table VI-5. Abundance and dispersion of hazel grouse winter food trees in three areas (two in Siberia and one in Sweden).

Category	Yana Valley N=140[a]	Dukcha Mtn N=180	Grimsö N=54
Preferred species			
Abundance (trees/ha)	204±24[b]	344±23	44±9
Dispersion (% plots present)	74%	100%	24%
Important species			
Abundance (trees/ha)	2952±169	831±84	308±31
Dispersion (% plots present)	99%	100%	79%

[a] Number of 10-m radius plots on wintering areas.
[b] Mean±SE.

other (Mann-Whitney tests, U values >7100, all P values <0.0001). The situation was similar for important species, except that food trees were more abundant in the Yana Valley (2952/ha) than on Dukcha Mountain (831); Grimsö again had the fewest food trees (308, Table V-5). These values were also all different (U values >6100, P values <0.0001).

The pattern of dispersion of food trees was highly clumped on the Grimsö area, as the distribution of both preferred and important food trees on the census plots was different from random (tested against a Poisson distribution; one-group χ^2=225.0 & 849.3, df=4 & 11, P<0.0001 in both cases) and the variance:mean ratio was greater than 1.0 (Zar 1974). This ratio was 8.7 for preferred trees and 13.3 for important trees. It was not possible to conduct this test on the data from the Yana Valley or Dukcha Mountain because the mean number of trees per plot was too high (Zar 1974). However, food appeared to be clumped there also, because the variance:mean ratios were high; 15.7 for preferred trees and 54.9 for important trees in the Yana Valley and 2.6 and 14.5, respectively, on Dukcha Mountain. The dispersion of food trees was compared among areas by comparing the frequency of plots containing food trees (Table VI-5). At Dukcha Mountain, preferred food trees occurred on all plots, significantly more than in the Yana Valley (χ^2_c=16.1, df=2, P<0.0001) and at Grimsö (χ^2_c=78.2, df=2, P<0.0001). Preferred trees were found on significantly more plots in the Yana Valley than at Grimsö (χ^2_c=65.4, df=2, P<0.0001). There was no difference in frequency of plots with important food trees between the Yana Valley and Dukcha Mountain (χ^2_c=0.004, df=2, P=0.95), and both areas had more than Grimsö (Yana, χ^2_c=33.9, df=2, P<0.0001; Dukcha, χ^2_c=12.1, df=2, P<0.001). Hazel grouse in the two Siberian areas not only had more food trees available to them than their Swedish counterparts, but this food was also more evenly distributed over the wintering areas.

DISCUSSION

The results of this study supported the predator hypothesis as the major factor promoting flocking in hazel grouse. As predicted by the predator hypothesis, groups were smaller in the thick spruce forests of Sweden, where cover was more available at foraging sites than in the open larch and deciduous forests in Siberia. This trend was also apparent within areas. In Siberia, flocks were smaller in larch-birch forests that contained a higher density of larch, which provided more cover than deciduous trees. Also, group size was not significantly different between two types of larch-birch forest. In Sweden, hazel grouse foraging as pairs used areas with less cover, fewer coniferous trees, and more deciduous trees than birds foraging alone. Thus, in all cases, greater numbers of hazel grouse were associated with less cover. That winter groups were significantly larger in the deciduous riparian forests than in the adjacent ecotonal larch-birch zone within the same areas (Yana and Omolon valleys) also indicated that group size was variable and related to forest type. Similarly, Hines (1986) and Bergerud & Gratson (1988) concluded that predation was the major factor promoting flock formation in grouse in general, by comparing flocking behavior and habitats of North American grouse.

Increased sociality can reduce vigilance time without increasing predation risk (Caraco 1979), but predation risk must be substantial before such increased protection can have any value and foraging time must be limited so the forager can benefit from reduced vigilance time (Ekman 1989a). Both conditions were met in Siberia. In addition to our observation, many cases of predation or attempted predation by goshawks on hazel grouse while they foraged arboreally have been documented (Donaurov 1947, Pynnönen 1954, Semenov-Tyan-Shanskii 1959, Gavrin 1969). Moreover, a rapid decline in the percentage of juveniles in shot samples over the winter in the Yana Valley suggested a relatively high winter mortality rate among this age group (Fig. VI-1). This decline also could be explained by a greater vulnerability of juveniles to shooting in late autumn than later. Generally, this does not seem to be the case in forest grouse, except for the large and late-maturing capercaillie (Tetrao urogallus) (Helminen 1963, Rusch et al. 1984, Hoffman 1985). Helminen (1963) and Hoffman (1985) concluded that the age ratios of hunter-killed forest grouse accurately reflected that in the population. Foraging time is limited for hazel grouse in Siberia during the winter. They spend on average 21.4-22.8 hr/day under the surface of the snow; more time is spent in snow during periods of colder ambient temperature (Andreev 1980). Food selection is also related to ambient temperature; in both the Omolon and Yana valleys, hazel grouse ate more Chosenia arbutifolia during colder weather, perhaps because they could forage more rapidly in this tree than in the others (Andreev 1979, 1980, Andreev & Drovetskii in prep.).

The results were not consistent with the food dispersion hypothesis. According to this hypothesis, groups should have been smallest and hazel grouse most territorial in Siberia where food was more abundant and more widely dispersed within hazel grouse winter habitat. The opposite was found, however. Social organization was clearly different in the two areas, with strong territoriality in Sweden (Chapter IV), and relatively cohesive flocks in the riparian forests of Siberia. The differences in food abundance and dispersion were striking, especially for preferred species (Table VI-5). The subalpine larch-birch forest on Dukcha Mountain had 7.8 times more preferred food trees per unit area than Grimsö, and the riparian forest on the Yana River had 4.6 times more. Just considering the important food trees, there were 9.6 times more on the Yana River and 2.7 times more on Dukcha Mountain than at Grimsö. Preferred food trees were found on every 314-m^2 plot on Dukcha Mountain and 74% of those along the Yana River, compared with only 24% within the wintering areas at Grimsö. Hazel grouse in the riparian forest on the Yana River did not select forests of any particular density for foraging, but Swedish grouse selected forests with fewer coniferous trees and more deciduous trees than expected. This probably reflected the more limited abundance and distribution of food in Sweden. To forage, Swedish grouse moved to areas with deciduous trees, but Siberian grouse were always surrounded by an abundance of deciduous trees, and presumably used greater group size to compensate for the lesser amount of cover.

Hazel grouse overwintered in much smaller groups in Sweden than in Siberia. These observations are consistent with the literature (Bergmann et al. 1982, Potapov 1989). However, we suggest that winter social organization is plastic in the hazel grouse; wintering as singles or pairs versus in large groups should not be viewed only as a difference in behavior between populations in the eastern and western Palearctic. There are few data in the literature that present mean group sizes to compare with our results. Volkov (1968) recorded a mean winter group size of 1.4 (the same as found in Sweden) in the spruce-dominated Central Forest Reserve of central European Russia, but most of the literature refers only to winter groups as singles/pairs or larger flocks. We have summarized these data from 27 areas (including our study areas) throughout the species' range, where both the most common group size and winter habitat were reported. These results were consistent with our conclusion that winter social organization in hazel grouse varies with forest type, and that larger flocks are characteristic of the riparian deciduous forests on large river systems in both the eastern and western Palearctic (Table VI-6). This suggests that the greater occurrence of groups in the eastern Palearctic is a result of the greater occurrence of large river systems with riparian forests there.

The stable flock sizes over winter, despite mortality, suggested an aggregation of flocks to maintain flock size, requiring a decline in the number of flocks over winter. Each forest type may have had a range of group sizes that provided the best protection from predators under the conditions of that habitat. The apparently higher mortality of juveniles in winter flocks is also found in other groups of flocking birds (Glase 1973, Ekman et al. 1981). Some positions in the flock, or microhabitats used by the flock, are more secure from predators than others, and the dominant members of the flock, usually adults, occupy these secure positions (Pulliam & Millikan 1982, Hogstad 1988, Ekman 1989a, 1989b). This leaves the subordinate (juvenile) individuals more vulnerable. The suggestion that juveniles occupied more vulnerable positions in the flocks remains the same whether the decline in percent juveniles in the shot sample was due to a greater vulnerability of the juveniles to natural predators or the hunter. It was not possible for us to determine if the hazel grouse in the flocks had a dominance hierarchy, but Sugimoto (1986) found a dominance hierarchy among female hazel grouse in winter in a captive flock of five females and one male. Dominance was related to size rather than age, as both the most and least dominant females were juveniles. If winter flocks of hazel grouse are dominance-structured, subdominates (especially juveniles) may join flocks for lack of a viable alternative (Ekman 1989b); it may be too dangerous to remain alone in the open forest, and the steep gradient between suitable habitat (riparian and ecotone forests) and unsuitable habitat (larch forest) limits their overwintering options.

Winter groups of two birds in Sweden and Siberia were almost always a male and a female; similarly, larger groups in Siberia were sexually mixed. This is different from most grouse, which winter in sexually segregated groups (Hines 1986).

In summary, all the available evidence supported the predation hypothesis

Table VI-6. Most common group size in winter among hazel grouse in relation to winter habitat in 27 localities throughout the species' range (based on 20 reports in the literature and this study).

Continent	Major habitat type	Most common group size Singles/pairs	 Larger	Sources[a]
Asia	Evergreen coniferous forests	3	0	A
	Larch-birch forests	4	0	B
	Deciduous riparian forests	0	5	C
Europe	Evergreen coniferous forests	14	0	D
	Deciduous riparian forests	0	1	E

[a] A=Larinov 1964, Bannikov 1957, Ismailov & Pavlov 1975.
B=Haga et al. 1987, this study (three sites).
C=Bannikov 1957, Mishin 1960, Babenko 1987, this study (two sites).
D=Donaurov 1947, Teidoff 1951, Pynnönen 1954, Semenov-Tyan-Shanskii 1959, Ivanter 1962, Rodionov 1963, Volkov 1968, Gavrin 1969, Glutz von Blotzheim 1973, Müller 1974, Scherzinger 1976, Zbinden 1979, Lennartsson 1983, this study (one site).
E=Donaurov 1947.

as the most important factor promoting flocking in winter by hazel grouse in some areas in Siberia. Gregariousness in hazel grouse, throughout its range and locally, appears to vary along a continuum of forest densities, with largest group sizes in the most open forest. The occurrence of relatively large and cohesive groups of hazel grouse in the riparian deciduous forests of Siberia is clearly homologous to the cooperation between male and female hazel grouse in exploiting more exposed food on winter territories in the spruce forest (Chapter V).

LITERATURE CITED

Andreev, A. V. 1979. Materialy po biologii teterevinykh ptits severo-vostochnoi Sibiri v zimnii period. Pp. 27-56 in A. V. Krechmar & F. B Chernyavskii, eds. Ptitsy severo-vostoka Azii. Dal'nevoctochnyi Hauchnyi Tsentp, Akademiya Nauk SSSR, Vladivostok. (In Russian)

Andreev, A. V. 1980. Adaptatsiya ptits k zimnim usloviyam Subarktiki. Nauka, Moscow. (In Russian)

Babenko, V. G. 1987. Zimnee naselenie ptits nizhnego Priamur'ya. Ornitologiya 22:160-166. (In Russian)

Bannikov, A. G. 1957. Zametki o zimnikh kormakh ryabchika i dayrskoi kuropatki v Kentee. Uchenye Zapiski Moskovskogo Gorodskogo Pedagogicheskogo Instituta Imini V. P. Potemkina 65:89-94. (In Russian)

Bergerud, A. T. & M. W. Gratson. 1988. Survival and breeding strategies of grouse. Pp. 473-577 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn, Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pp. 64-96 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford.

Brown, J. L. & G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-263.

Caraco, T. 1979. Time budgeting and group size: a test of theory. Ecology 60:618-627.

Clark, C. W. & M. Mangel. 1986. The evolutionary advantages of group foraging. Theor. Pop. Biol. 30:45-75.

Davies, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 _in_ J. R. Krebs & N. B. Davies, eds. Behavioural ecology--an evolutionary approach. Blackwell Sci. Publ., Oxford.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika 4:77-122. (In Russian)

Ekman, J. 1989a. Ecology of non-breeding social systems of _Parus_. Wilson Bull. 101:263-288.

Ekman, J. 1989b. Group size in dominance-structured populations. Ornis Scand. 20:86-88.

Ekman, J., G. Cederholm & C. Askenmo. 1981. Spacing and surivival in winter groups of willow tit _Parus montanus_ and crested tit _Parus cristatus_--a removal study. J. Anim. Ecol. 50:1-9.

Elgar, M. A. 1986. The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. Behav. Ecol. Sociobiol. 19:433-438.

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Gaidar, A. A. & B. M. Zhitkov. 1974. Method of determining age of hazel hen. Soviet J. Ecol. 5:290-291.

Gavrin, V. F. 1969. Ekologiya ryabchika v Belovezhskoi Pushche. Gosudarstvennoe Zapovedno-Okhotnich'e Khozyaistvo "Belovezhskaya Pushcha" 3:146-172. (In Russian)

Glase, J. 1973. Ecology of social organization in the black-capped chickadee. Living Bird 12:235-267.

Glutz von Blotzheim, U. N., K. M. Bauer & E. Bezzel. 1973. Handbuch der Vögel Mitteleuropas. Band 5, Galliformes und Gruiformes. Akademische Verlagsgesellschaft, Frankfurt am Main.

Gosling, L. M. & M. Petrie. 1981. The economics of social organization. Pp. 315-382 _in_ C. R. Townsend & P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Haga, R., S. Yokota & S. Takamata. 1987. Ecology and breeding biology of the hazel grouse _Tetrastes bonasia_ in captivity; 2. Home range, circadian rhythm and roosting behavior in winter in eastern Hokkaido. Jap. J. Ornithol. 35:145-154. (In Japanese, English summ.)

Helminen, M. 1963. Composition of the Finnish populations of capercaillie, Tetrao urogallus, and black grouse, Lyrurus tetrix, in the autumns of 1952-1961, as revealed by a study of wings. Pap. Game Res. 23:1-124.

Hines, J. E. 1986. Social organization, movements, and home ranges of blue grouse in fall and winter. Wilson Bull. 98:419-432.

Hoffman, R. W. 1985. Blue grouse wing analyses: methodology and population inferences. Colorado Div. Wildl., Spec. Rep. No. 60.

Hogstad, O. 1988. Rank-related resource access in winter flocks of willow tit Parus montanus. Ornis Scand. 19:169-174.

Hosmer, D. S. & S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York.

Huempfner, R. A. & J. R. Tester. 1988. Winter arboreal feeding behavior of ruffed grouse in east-central Minnesota. Pp. 122-157 in A. T. Bergerud & M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Ismailov, I. V. & M. P. Pavlov. 1975. Predbaikal'e i Zabaikal'e. Pp. 100-112 in S. V. Kirikov, ed. Teterevinye ptitsy. Nauka, Moscow. (In Russian)

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In Russian)

Krebs, J. R. and C. J. Barnard. 1980. Comments on the function of flocking in birds. Proc. Intern. Ornithol. Congr. 17:795-799.

Kuusela, K. 1990. The dynamics of boreal coniferous forests. Finnish Nat. Fund Res. Devel., Helsinki.

Larinov, G. P. 1964. K biologii kamennogo glukharya i ryabchika v tsentral'noi Yakutii. Uchenye Zapiski Yakutskogo Gosudarstvennogo Universiteta 15:91-96. (In Russian)

Lennartsson, T. 1983. Järpens biologi och beståndstäthet i Västmanland. Fåglar i Västmanland 14:64-72. (In Swedish)

Marzluff, J. M. & R. P. Balda. 1988. Resource and climatic variability: influences on sociality of two southwestern corvids. Pp. 255-283 in C. N. Slobodchikoff, ed. The ecology of social behavior. Academic Press, Inc., New York.

Metcalfe, N. B. 1989. Flocking preferences in relation to vigilance benefits and aggression cost in mixed-species shorebird flocks. Oikos 56:91-98.

Mishin, I. P. 1960. K biologii teterevinykh ptits na Sakhaline. Ornitologiya 3:251-258.

Moriarty, D. J. 1976. The adaptive nature of bird flocks: a review. Biologist 58:67-79.

Müller, F. 1974. Haselhuhn, das vergessene Wild. Pirsch 26:1043-1047.

Neu, C. W., C. R. Byers & J. M. Peek. 1974. A technique for analysis of utilization--avalability data. J. Wildl. Manage. 38:541-545.

Orians, G. 1971. Ecological aspects of behavior. Avian Biol. 1:513-546.

Potapov, R. L. 1989. Gattung Bonasa Stephens, 1819. Pp. 103-116 in R. L. Potapov & V. E. Flint, eds. Handbuch der Vögel der Sowjetunion, Band 4 Galliformes und Gruiformes. A. Ziemsen Verlag, Wittenberg Lutherstadt, DDR.

Pulliam, H. R. & G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biol. 6:169-197.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Rodionov, M. A. 1963. K biologii ryabchika (Tetrastes bonasia L.) Leningradskoi Oblasti. Leningradskii Gosudarstvennyi Pedagogicheskii Institut Imeni A. I. Gertsina Uchenye Zapiski 230:139-165. (In Russian)

Rusch, D. H., S. DeStefano & R. J. Small. 1984. Seasonal harvest and mortality of ruffed grouse in Wisconsin. Pp. 137-150 in W. L. Robinson, ed. Ruffed grouse management: state of the art in the early 1980's. BookCraft Printers, Chelsea, Michigan.

Scherzinger, W. 1976. Raufuß-Hühner. Schriftenreihe des Bayerischen Staatsministeriums für Ernährung, Landwirtschaft und Forsten, Nationalpark Bayerischer Wald 2:1-71.

Semenov-Tian-Shanskii, O. 1959. Ekologiya teterevinykh ptits. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1-318. (In Russian)

Sugimoto, M. 1986. Captive breeding and behavioral analysis of the hazel grouse Tetrastes bonasia. Thesis, Obihiro Univ. of Agr. and Vet. Med., Obihiro, Japan.

Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse Bonasa bonasia in spring and autumn. Ornis Fennica 68:in press.

Teidoff, E. 1951. Zur Ökologie, Biologie und Psychologie des Haselhuhns (Testrates [sic] bonasia). Bonn. Zool. Beitr. 2:99-108.

Volkov, N. I. 1968. Izmenenie chislennosti ryabchika zimoi. Pp. 8-9 in S. V. Kirikov & O. N. Shubnikova, eds. Resursy teterevinykh ptits v SSSR. Nauka, Moscow. (In Russian)

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Zbinden, N. 1979. Zur Ökologie des Haselhuhns Bonasa bonasia in den Buchenwäldern des Chasseral, Faltenjura. Ornithol. Beob. 76:169-214.

VII. THE IMPORTANCE OF ALDER TO HAZEL GROUSE IN FENNOSCANDIAN BOREAL FOREST: EVIDENCE FROM FOUR LEVELS OF SCALE

INTRODUCTION

The social organization of a species can be viewed in part as an adaptation to prevailing environmental conditions (Marzluff and Balda 1988). One such condition, shown to be important for social organization during the nonreproductive period, is the abundance and availability in space and time of winter food (Davies 1978, Pulliam and Millikan 1982, Stamps and Tollestrup 1984, Marzluff and Balda 1988). Abundance of winter food has also been proposed as an important factor limiting breeding densities of many birds (Fretwell 1972). The winter diet of most species of grouse consists of one or two food species that are dominant, or at least abundant, in the winter habitat (Doerr et al. 1974, Moss & Hanssen 1980). The hazel grouse (Bonasa bonasia), a Palearctic grouse that inhabits boreal and montane forests, differs from other grouse in using a winter food that is relatively uncommon in boreal forests, the staminate catkins and buds of alder (Alnus spp.) (reviews in Bergmann, et al. 1982, Jacob 1988). In fact, Bergmann, et al. (1982) stated that "das Haselhuhn" should actually have been called "das Erlenhuhn"--the alder grouse. When snow covers the ground, hazel grouse are restricted to an arboreal diet (Salo 1971, Ahnlund & Helander 1975). If the abundance and dispersion pattern of winter food is a factor influencing the winter social organization of grouse, then hazel grouse would be expected to differ from the other species. This is the case, as the hazel grouse is one of the few species exhibiting territoriality in winter (Bergmann et al. 1982). But, this conclusion would be premature, because no studies have examined how closely hazel grouse numbers and distribution are dependent upon the abundance and distribution of alder, or to what degree hazel grouse actually select alder over the other available winter food resources. Hazel grouse in southern Finland foraged in alder more than expected in winter and foraged more in alder than in birch (Uusvaara 1963), but studies in northern Finland and near the Ural Mountains have shown that hazel grouse ate more birch (Betula spp.) than alder (Donaurov 1947, Salo 1971).

A problem to consider when studying ecological patterns and processes is that they are virtually all scale-dependent. Differences in scale are important because they affect the results obtained and how they are interpreted (Newton 1980, Addicott et al. 1987, Wiens 1989). Although there are relatively few studies of the effects of scale on the patterns of habitat association, some have shown differing results depending on the scale of the study (Hengeveld 1987, Morris 1987, Gutzwiller & Anderson 1987, Wiens 1989). Wiens (1989) recommended a focus on the individual or local population scale for investigations of the responses of individuals or populations to spatial variations in resources, but added that some perspectives from the other scales also would be helpful. This approach was followed in this study.

The purpose of this study was fourfold: 1) to determine if alder actually was the preferred winter food by a local population of hazel grouse, 2) to document the abundance and dispersion pattern of alder on the area, 3) to test if hazel grouse territories can be considered defended feeding territories, ie. territory size is related to both food density and competitor density (Hixon 1980, Gauthier 1987), and 4) to determine if the abundance and/or distribution of hazel grouse varies with abundance or distribution of alder over the scales recommended by Wiens (1989:235). These scales are: space occupied by a single individual (territory), local patch, region containing many patches (called landscape here), and biographical scale large enough to encompass different climates, vegetation formations and assemblages of species. This study was limited to Fennoscandian boreal forest because some hazel grouse populations outside of this area depend on food trees other than alder or birch in winter (Bergmann, et al. 1982, Jacob 1988).

STUDY AREA

The study area (285 ha) was about half the forest reserve located on the Grimsö Wildlife Research Area (140 km^2) in southcentral Sweden (59-60° N and 15-16° E). Most of the forest burned during a fire in 1914. The area has received very little forestry management since 1972. It was dominated by Norway spruce (Picea abies, 56% of trees), white birch (Betula pendula) and pubescent birch (B. pubescens, together 23%), and Scots pine (Pinus sylvestris, 15%). Other deciduous trees (6%) included aspen (Populus tremula), black alder (Alnus glutinosa), great willow (Salix caprea), and rowan (Sorbus aucuparia). Gray alder (A. incana) and bird cherry (Prunus padus) were rare on the area. The remaining 237 ha of the reserve had a lower proportion and variety of deciduous trees. The dominant field layer species throughout the reserve were billberry (Vaccinium myrtillus), cowberry (V. vitis-idaea), and wavy hairgrass (Deschampsia flexuosa).

Most of the Grimsö Wildlife Research Area is intensively managed industrial forest. It is relatively flat, 100-150 m in elevation, and dominated by forest (72%) and bogs (18%). Pine and spruce are the most common trees; deciduous trees are much less common than on the reserve. A more detailed description is found in Cederlund (1981).

METHODS

I captured hazel grouse on the study area by luring or chasing them into nylon fishing nets, radio-marked them with necklace-type transmitters (Kenward 1987), and relocated them 3-6 times a week during three winters (1 November-31 March 1987-88 to 1989-90). I determined the use of winter arboreal foods by observing radio-marked birds while they foraged, and recording location in the canopy, species of tree, height of tree, and distance from spruce forest for each tree in which grouse foraged. When determining distance from spruce forest, I arbitrarily considered such trees to be outside the spruce forest if they were in openings at least 10 by 40 m in size. I also recorded the species of 124 deciduous trees at 11 known feeding sites that were judged to be fed in by hazel grouse, based on the presence of dispersed woody droppings of hazel grouse under them in November 1987.

I determined the size of 20 winter territories of 15 radio-marked grouse, for which at least 25 locations were available, based on the modified minimum area method (Harvey & Barbour 1965). Hazel grouse defend territories from other members of the same sex during winter (Chapter IV). Three areas totalling 71.2 ha were not included within any of these territories. Moreover, they probably were not included within the territories of unmarked birds, because neither hazel grouse nor their tracks were observed there, despite several searches during periods of snow cover in these winters.

A description of the forest on the intensive study area was based on 10-m radius plots as recommended by Marcström, et al. (1983). The plots were located systematically at a density of two per ha. Among other things, all trees (>3 m high) were counted, canopy height measured, canopy density estimated to the nearest 10%, basal area of trees measured using a relascope, coverage of field layer vegetation estimated to the nearest 10%, soil moisture and fertility determined, based on the field layer vegetation (Hägglund & Lundmark 1984), and vegetative cover at 0-2.5 m estimated using a cover board (Nudds 1977). Forest age was obtained from forestry maps. In addition, all wet areas were visited within the entire reserve, all alders counted, classified into height classes (<3 m, 3-10 m, >10 m) and distance from spruce forest (within, 1-15 m, >15 m) and recorded by 1-ha blocks. Wet areas were visited because alders, especially black alder, require wet areas (Børset 1985). The number of "preferred alders" (defined in results) within each territory was estimated by overlaying a map of the territory upon a map of the distribution of alders. For the 1-ha blocks not completely included within a territory, I assumed that the territory included 75% of the alders within the block if more than 50% of the block was within the territory, and 25% if less than 50% was within it.

Territorial male hazel grouse were counted on the entire forest reserve (522 ha) during spring and autumn by recording their response to an imitated territorial song, using 6-min count periods from points placed at 150-m intervals. This method is about 80-85% effective (Swenson 1991). Winter density was determined to compare with territory size. It was the mean of autumn and spring density on the study area (western half of the reserve), where territory sizes also were determined.

Hazel grouse distribution on the entire Grimsö Wildlife Research Area (140 km^2) was determined from casual wildlife observations mapped weekly from 1977 to 1987 on a 1:50,000 scale map by personnel at the station. Observations were separated into winter (1 November-31 March) and nonwinter. Alder distribution was determined by asking 10 researchers and assistants, each with at least 10 years experience at the station, to draw the occurrence of alder on maps (also 1:50,000). A composite map was made from these, and the entire area was divided into 25-ha blocks for analysis.

Densities of hazel grouse and alder were also compared throughout Finland. Mean summer densities of hazel grouse from 1964 to 1977, determined using the same technique (transect counts) over the entire country, were obtained for 15 areas from Lindén & Rajala (1981). Forestry statistics, the amount of forest dominated by alder and "other deciduous trees", which were almost all birch, was obtained for 19 areas from Anonymous (1977). These data were combined into 13 areas covering all of Finland except the Åland Archipelago. Where two or three areas had to be combined to compare these data sets, an unweighted mean was used.

Annual variation in production of staminate catkins was estimated each January from 18 black alder trees on the study area using a modification of the technique of Svoboda & Gullion (1974). These trees were ca. 50 m from spruce forest (too far to be used by hazel grouse). The catkin index was the sum of catkins on 5 upper branches of all the trees. Total production of staminate catkins and buds was determined from three black alder trees cut down in late December 1988 in Halden, Norway. These alders were all 50-52 years old and 15-17 m high. All buds and catkins were removed and counted from every other branch from three equal canopy height categories. A sample of 20 of each of the bud types and catkins for each tree and height category were weighed to the nearest 0.1 milligram following drying at 40° C for 72 hrs. These alders were within spruce forest, but were in an urban area without hazel grouse. Years of high and low catkin production were the same at Grimsö and Halden (pers. obs.).

Dispersion patterns were examined for randomness by testing against a Poisson distribution (Zar 1974). If significantly different from random, a variance:mean ratio >1 indicated a clumped distribution and <1 indicated a regular distribution (Zar 1974). A 5% level was accepted as sufficient to reject a null hypothesis. $\underline{X}^2$ tests using a 2x2 contingency table were corrected for continuity with Yate's correction (Zar 1974). Means are presented with standard errors of the mean.

RESULTS

Selection of winter food trees by hazel grouse

Each winter, hazel grouse foraged more in alders than in other genera of trees (Table VII-1). Data from the 1987-88 winter included observations of foraging birds (N=66) and trees under which hazel grouse droppings were found (N=57). These two sources of data were combined because no difference was found in the proportion of genera used ($\underline{X}^2$=1.49, df=2, P=0.48). The use of alder (74%) was greater than expected from its availability on the area, as it comprised only 5.8% of the deciduous trees (one group $\underline{X}^2$=1535.9, df=3, P<0.0001; Salix, Prunus, Sorbus, and Quercus were combined due to low expected values).

The alder catkin index, based on catkin counts on marked trees, was 524 in 1987-88. It increased 15 times to 7695 in 1988-89 (paired t test, t=4.05, df=17, P<0.001), declined 81% to 1430 in 1989-90 (paired t =3.95, P=0.001), and increased 400% to 5816 in 1990-91 (paired t=4.71, P=0.0002). These annual differences were also easily observable in the surrounding forest. The winter in which both alder and birch had poor crops of catkins (1987-88) was also the only winter that hazel grouse were observed foraging in trees other than alder or birch. In 1988-89, when there was an abundance of alder catkins but few birch catkins, alder received its highest level of use. In 1989-90, when

Table VII-1. Use of deciduous trees by foraging hazel grouse relative to their occurrence on the study area over three winters.

	Trees (%)				
	Used				Available
	1987-88	1988-89	1989-90	Total	
Genus	N=123	N=24	N=37	N=184	N=4922
Alnus	74	83	65	74	5.8
Betula	17	17	35	23	83.9
Populus	5	0	0	1.7	7.3
Salix	2	0	0	0.7	0.9
Prunus	1	0	0	0.3	0.1
Sorbus	1	0	0	0.3	0.2
Quercus	0	0	0	0	0.02

there was an abundant crop of birch catkins, but few alder catkins, birch received its highest level of use. This suggested that hazel grouse selection of foraging trees was influenced by the abundance of catkins. The use of tree genera for foraging (testing the groups alder, birch, and other trees) was different in 1987-88, when the alder and birch had few catkins, than in the other years ($\underline{X}^2=17.87$, df=2, $P<0.0001$, Table VII-1). However, no difference was detected between 1988-89 and 1989-90 ($\underline{X}^2_c=1.64$, df=1, $P=0.20$).

Hazel grouse did not appear to choose between species within the genera *Alnus* and *Betula*, based on trees with hazel grouse droppings under them that were examined in November 1987. For birch, 13% of 48 pubescent birch and 9% of 33 white birch had been used ($\underline{X}^2_c=0.01$, $P=0.90$). The results were similar for alder, 61% of 23 black alder and 50% of 6 gray alder had been used ($\underline{X}^2_c=0.0003$, $P=0.99$).

Hazel grouse preferred to forage in tall trees that were near spruce forest. The mean height of alders used for foraging was 16.3±0.4 m (N=89), of which 94% were ≥10 m or taller. In a sample of 6810 alders >3 m tall on the study area, 55.2% were estimated to be ≥10 m, significantly less than the trees used by foraging grouse (one group $\underline{X}^2=55.33$, df=1, $P<0.0001$). The height of birches used for foraging (16.8±0.6 m, N=24) did not differ from that for alders ($t=0.62$, df=111, $P=0.53$).

Of 91 alder trees used for foraging, 36% were surrounded by spruce forest, another 33% were outside spruce forest, but <5 m away, and 19% were 5-10 m away from spruce, for a total of 88% within 10 m of spruce forest. The farthest an arboreally foraging hazel grouse was seen from spruce forest was 22 m. This was significantly different from the distance of all alders from spruce forest (one group $\underline{X}^2=70.6$, df=4, $P<0.0001$, Fig. VII-1). Trees ≤15 m were used more than expected, whereas those >15 m from spruce forest were used less. Throughout this paper, "preferred alders" will refer to alders that are >10 m tall and ≤15 m from spruce forest. There was no statistical difference in mean distance of foraging tree from spruce forest between alders (4.3±0.5 m, N=91) and birches (6.2±1.2 m, N=25, $t=1.80$, df=114, $P=0.08$).

Catkins were largest in the middle and upper thirds of the alder canopies (Table VII-2). Catkins, lateral and terminal buds were all distributed unevenly within the alder canopy, occurring more than expected in the upper and middle thirds (Table VII-2). The standing crop of catkins and buds from three black alder trees cut down in December 1988 averaged 547 g catkins and 227 g buds dry weight (Table VII-2). The weights of 20 buds of each type (lateral and terminal) from each of three canopy height classes and the three trees was analyzed using a three-way ANOVA. No differences were found between bud types ($F<0.00001$, df=1, $P=1.00$), height classes ($F=2.01$, df=2, $P=0.14$), nor trees ($F=1.2$, df=2, $P=0.31$). However, a two-way ANOVA showed differences in the dry weights of staminate catkins from individual trees ($F=14.5$, df=2, $P<0.0001$), height classes ($F=20.2$, df=2, $P<0.0001$), and their interaction ($F=4.9$, df=4, $P<0.001$).

Hazel grouse preferred to forage in the upper parts of tree canopies (one group $\underline{X}^2=10.3$, df=2, $P=0.006$, Table VII-3). Data were combined because

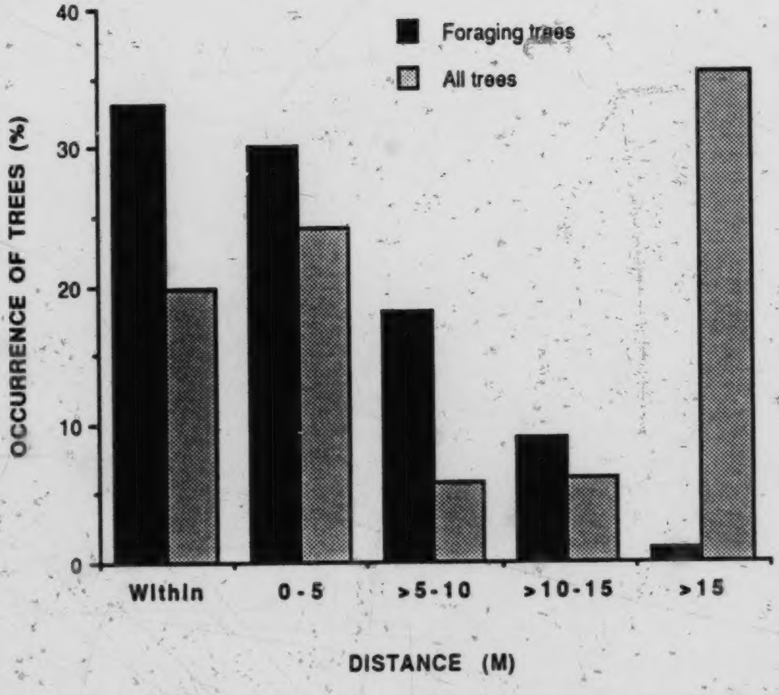

Fig. VII-1. Occurrence of alders used by foraging hazel grouse and all alders >10 m tall in relation to distance from spruce forest on the study area in southcentral Sweden.

Table VII-2. Number and biomass of staminate catkins and buds within the crowns of three black alder trees from Halden, Norway, winter 1988-89. (Difference refers to effect of position in canopy.)

	Position in canopy (in thirds)			
Category	Top	Middle	Bottom	Difference
Staminate catkins				
Mean mass (g)	0.191	0.182	0.116	<0.0001[a]
Distribution (%, N=10,075)	36	39	25	<0.0001[b]
Biomass per tree, (g)	232	239	97	
Biomass (%)	41	42	17	
Lateral buds				
Mean mass (g)	0.023	0.027	0.027	>0.05[c]
Distribution (%, N=19,172)	37	37	26	<0.0001[b]
Biomass per tree (g)	54	64	44	
Biomass (%)	33	40	27	
Terminal buds				
Mean mass (g)	0.029	0.028	0.030	>0.05[c]
Distribution (%, N=6,033)	38	41	21	<0.0001[b]
Biomass per tree (g)	22	23	13	
Biomass (%)	38	40	22	
All buds				
Biomass per tree (g)	76	87	57	
Biomass (%)	35	40	26	

[a] two-way ANOVA (tree, canopy height class, N=20 per cell).
[b] one-group $\underline{X}^2$.
[c] three-way ANOVA (tree, canopy height class, bud type).

Table VII-3. Location of foraging hazel grouse in tree canopies in winter, Grimsö Wildlife Research Area.

	Percent of observations		
Height in tree	Alder (N=74)	Birch (N=23)	Combined (N=97)
Top third	42	52	44
Middle third	36	39	37
Bottom third	22	9	19

location in a tree did not differ between alder and birch (X^2=2.0, df=2, P=0.36). The location of foraging grouse within the canopy of alders (Table VII-3) was not different from that expected, based on the distribution of catkin biomass (one group X^2=1.47, df=2, P=0.48) or bud biomass (one group X^2=1.77, df=2, P=0.41).

Dispersion pattern and habitat of black alder

The dispersion of alder on the study area was determined by using 566 systematically-placed plots of 10-m radius. Of these, 505 contained no alder over 3 m tall, 17 contained 1, 11 contained 2, and 44 contained more than 3, giving a mean of 0.50 trees per plot. This distribution differed from random (Poisson distribution, one group X^2=814.4, df=5, P<0.0001); the pattern of dispersion was clumped because the variance:mean ratio was 8.5 (Zar 1974). The distribution of alder also appeared to be clumped over the entire Grimsö Wildlife Research Area (Fig. VII-2).

During the survey of alders on the study area, 6810 trees >3 m tall were counted. Of these, 3762 (55.2%) were of the preferred height (>10 m), but only 2306 (61.3% of tall trees) were <15 m from spruce forest. Thus, only 33.9% of all alders >3 m tall on the study area fell into the preferred category.

Alder trees >3 m tall occurred on 11% of the 10-m radius plots on the study area. An analysis of habitat variables associated with alder showed that soils were wetter and more fertile, as determined by field vegetation, and that they were found in younger forests than expected (Table VII-4). Some variables such as total tree density, basal area, canopy height, canopy density, and vegetative cover at 0-2.5 m did not appear to influence the presence of alder. Alder occurred in association with other hazel grouse food species requiring rich and moist soils, ie. birch, rowan, bird cherry, great willow, and total density of rich forbs, but was negatively associated with other food species requiring drier and/or poorer soils, ie. aspen, bilberry and cowberry. No correlation was found between the density of alder and spruce.

Distribution of alders and hazel grouse: level of territory (ca 20 ha)

The high preference for alders suggested that winter territories should be located at concentrations of alders. This was the case. Winter territories contained 7.8 preferred alders per ha (unweighted means for males and females). However, the 72 ha not used by hazel grouse in winter contained only 0.8 preferred alders per ha.

Winter territory size differed between sexes; female territories (22.5±1.4 ha, N=6) were 37% larger than those of males (16.4±1.6 ha, N=14, t=2.36, df=1, P=0.03). However, female territories contained, on average, only 18% more preferred alders (161±16.5) than male territories (136±14.5 alders, t=0.98, df=19, P=0.34). Average winter territories, sexes combined, each contained a mean of 144±11 preferred alders; the fewest preferred alders in a territory was 82. It was predicted that size of winter territories, sexes combined, would correlate negatively with density of alders and population density. Only density of alders entered significantly into a stepwise multiple regression (F=11.27,

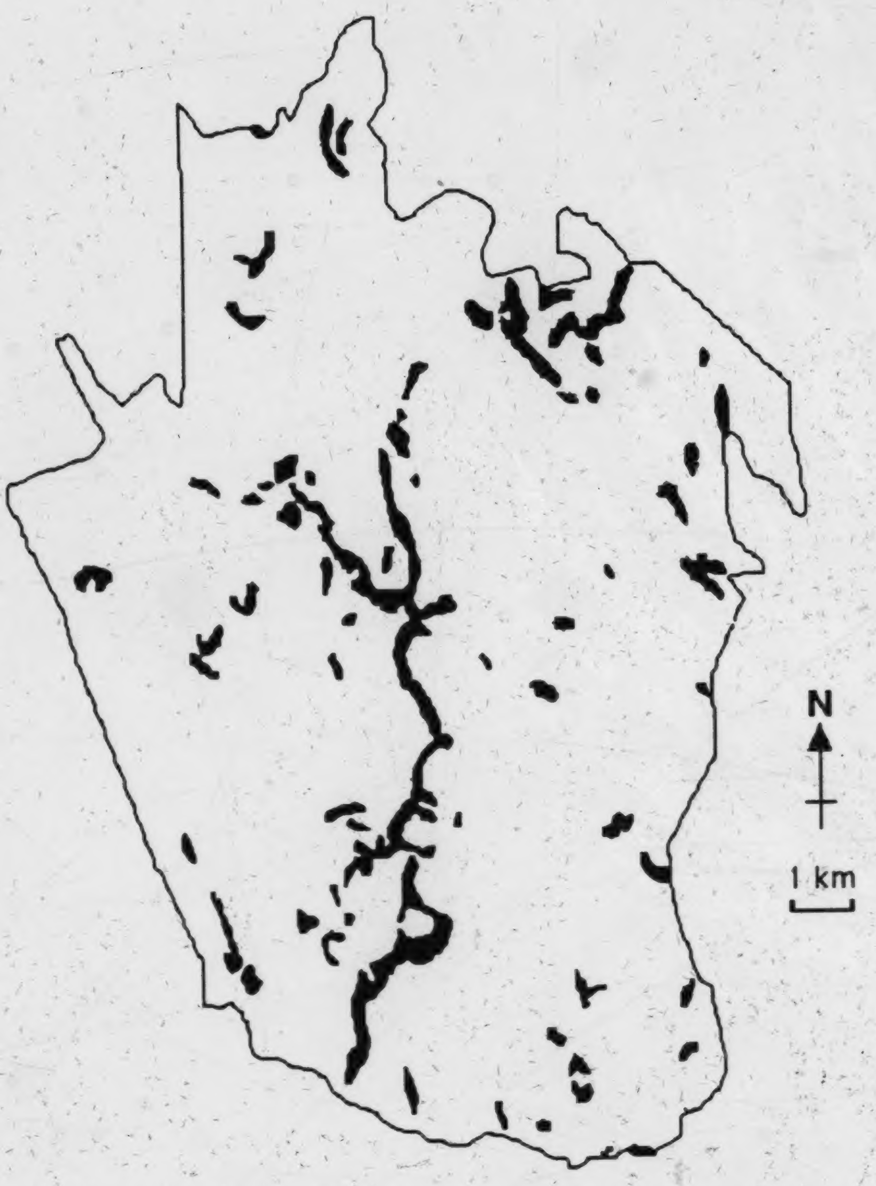

Fig. VII-2. Distribution of alder on the Grimsö Wildlife Research Area.

Table VII-4. Selected habitat variables relative to the occurrence of alder trees (>3 m tall) on 566 plots on the study area, Grimsö Wildlife Research Area.

Habitat variable	Mean values in areas		P[a]
	With alder	Without	
Soil moisture (class, 1=driest)	2.66	2.24	***
Soil fertility (class, 1=richest)	4.4	5.5	***
Forest age (yrs)	62	69	*
Total tree density (per plot)	34.8	31.2	ns
Basal area of trees (m^2/ha)	20.8	19.6	ns
Canopy height (m)	16.7	16.5	ns
Canopy density (%)	60.4	56.1	ns
Cover at 0-2.5 m (score)	58.5	60.1	ns
Spruce density (per plot)	15.7	17.9	ns
Pine density (per plot)	2.2	5.2	***
Birch density (per plot)	11.1	6.8	***
Rowan density (per plot)	0.4	0.1	***
Aspen density (per plot)	0.1	0.7	*
Bird cherry density (per plot)	0.05	0.002	**
Great willow density (per plot)	0.2	0.07	***
Bilberry coverage (%)	5.1	19.0	***
Cowberry coverage (%)	3.0	5.9	***
Total forb coverage (%)	3.9	1.0	***

[a] P based on Mann-Whitney U tests; ns means P>0.05, * means P<0.05, ** means P<0.01, and *** means P<0.001.

df=1,18, P=0.0035, Fig. VII-3); but the contribution of population density to the regression was almost significant (F=3.55, df=1, 18, $P<0.10$). Together, these variables explained about one half of the variation in territory size (multiple regression, $r^2=0.49$, df=18, one-tailed P=0.002). There was no relation between alder catkin index and territory size ($r^2=0.06$, df=18, two-tailed P=0.30).

Abundance of alders and hazel grouse: level of local patch (5 km^2)

As territories contained about 10 times more preferred alders than forest without territories, it follows that an area with fewer preferred alders should have fewer hazel grouse. On the forest reserve within the Grimsö Wildlife Research Area, the western half (the study area) contained significantly more preferred alders (5.5±0.7 per surveyed ha, N=326) than the eastern half (1.9±0.8 per ha, N=277; Mann-Whitney test, U=26155, $P<0.0001$), as well as a higher proportion (42%) of 1-ha plots with preferred alders than the eastern half (12%). Hazel grouse density was consistently lower in the eastern half during 6 censuses (Fig. VII-4, Wilcoxon signed test, P=0.028).

Distribution of alders and hazel grouse: level of landscape (140 km^2)

Within the entire Grimsö Wildlife Research Area, observations of hazel grouse were related to the presence of alder (Table VII-5). Hazel grouse were observed more often in 25-ha blocks that contained alder or bordered a block containing alder in both winter (one group $\chi^2=23.1$, df=2, $P<0.0001$) and the rest of the year (one group $\chi^2=46.2$, df=2, $P<0.0001$). The difference between winter and the rest of the year was not significant ($\chi^2=3.7$, df=2, P=0.15).

Abundance of alder and hazel grouse: level of biogeographic region (337,000 km^2)

The only large area with data on hazel grouse densities and alder densities is Finland. Mean densities of hazel grouse in summer during 1964-1977 were compared with the proportion of the forest dominated by alder and birch in 13 areas of Finland. Hazel grouse densities were positively correlated with the arcsine transformed estimate of alder abundance ($r^2=0.603$, df=11, one-tailed P=0.002, Fig. VII-5.). Even when the northernmost area in Finland was excluded, because this is the edge of the range of both hazel grouse and alder and other factors could be reducing both species there, the relationship was still significant ($r^2=0.29$, df=10, one-tailed P=0.035). No relationship, however, was found between hazel grouse density and birch abundance ($r^2=0.045$, two-tailed P=0.49, Fig. VII-6).

DISCUSSION

Selection of winter food

Hazel grouse preferred to forage in alder in winter, although they did not seem to differentiate between species in the genus. A preference for alder was recorded in years with both abundant and few catkins (Table VII-1). Both species of birch appeared to be a secondary winter food, whereas the group

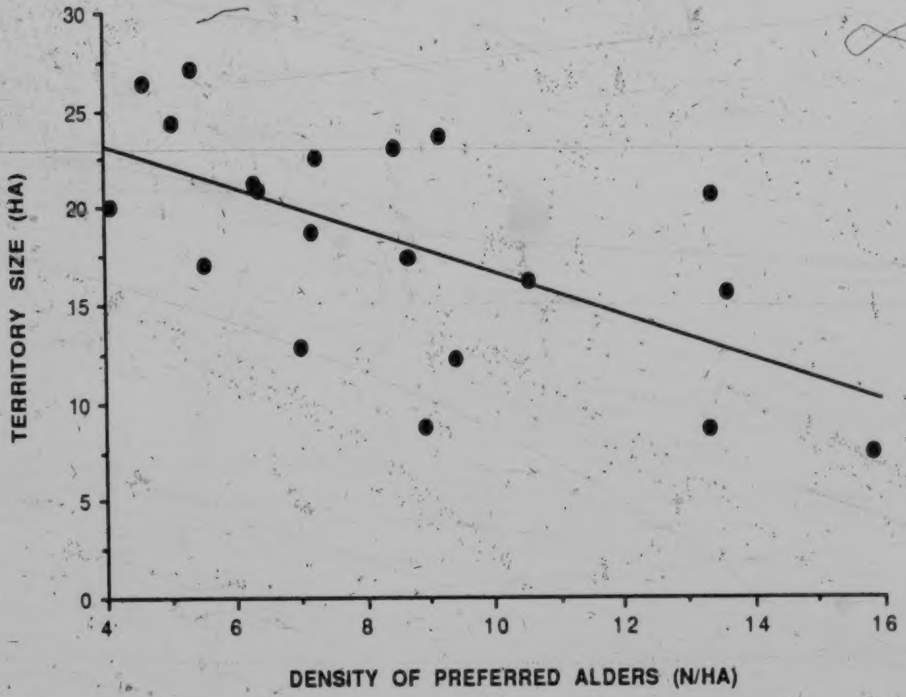

Fig. VII-3. Relationship between winter territory size and density of preferred alders on the study area ($r^2=0.385$, df=18, one-tailed $P=0.002$).

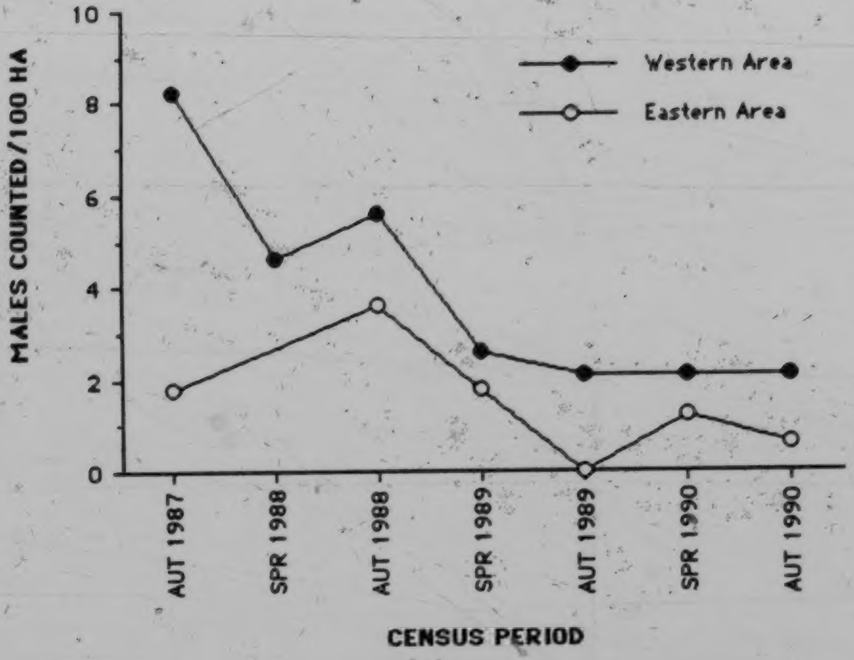

Fig. VII-4. Counts of territorial male hazel grouse on the western and eastern halves of the forest reserve, Grimsö Wildlife Research Area (A=autumn, S=spring, no count on eastern half in spring 1988).

Table VII-5. Distribution of hazel grouse relative to the distribution of alder on 25-ha blocks within the Grimsö Wildlife Research Area (data from 1977-1987).

	Distribution of blocks (percent)		
	Blocks with Hazel grouse		Total blocks
Type of block	In winter (N=52)	Rest of year (N=129)	(N=539)
Contained alder	62	60	32
Bordered a block with alder	37	29	48
Far (≥500 m) from alder	2	10	19

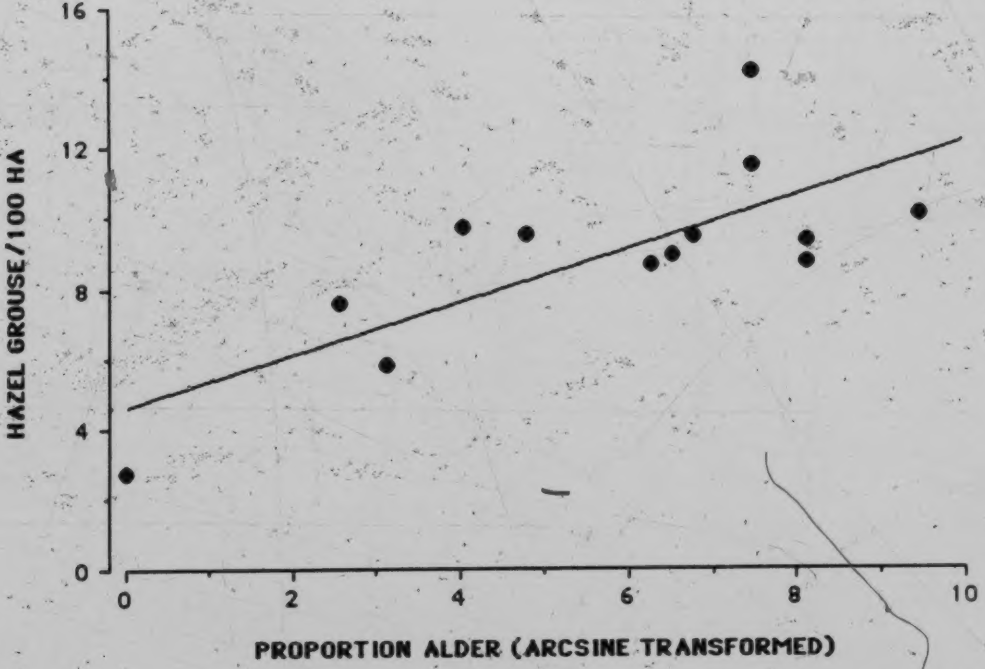

Fig. VII-5. Relationship between mean relative hazel grouse density from 1964 to 1977 and proportion of forests dominated by alder in Finland (r^2=0.603, df=11, one-tailed P=0.002).

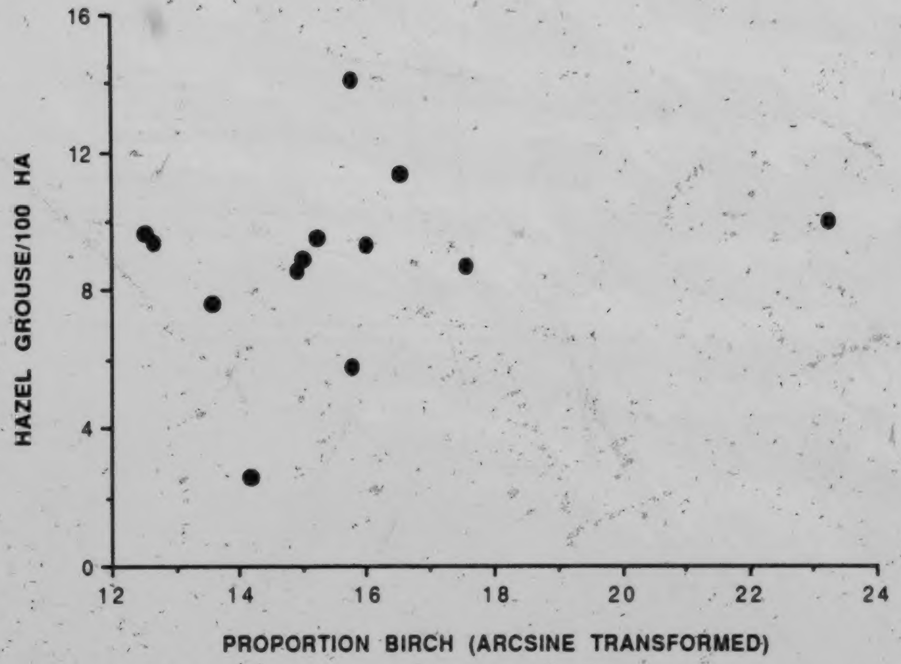

Fig. VII-6. Relationship between mean relative hazel grouse density from 1964 to 1977 and proportion of forests dominated by birch in Finland ($r^2=0.045$, df=11, two-tailed $P=0.49$).

aspen, great willow, bird cherry, and rowan formed a tertiary food source. Although birch was used less than expected, based on its availability, than these other four species, it was more important to the hazel grouse because of its greater availability and the observation that these tertiary food species were used only when both alder and birch had few catkins (Table VII-1). Uusvaara (1963) reported that hazel grouse fed in alders more and birch less than expected based on their abundance in southern Finland, but Salo (1971) found that hazel grouse in far northern Finland, an area with little alder, fed primarily on birch in winter. Analyses of the catkins and buds of gray alder and pubescent birch showed that they had similar chemical and caloric contents, which led him to conclude that "in areas where grey alder does not occur, birch apparently replaces it without causing any deficiencies in the bird's diet" (Salo 1973:386). Salo's study area was perhaps marginal for hazel grouse, occurring north of the species' limit of continuous distribution in Finland (Lindén 1983). Nevertheless, his results suggest that nutrition may not be the most important reason for the high preference shown for alder over birch. Whatever the reason, the high preference I found indicates that there must be an advantage to forage on alder rather than birch.

Alder and birch, particularly the catkins, provide a very nutritious food, the most protein-rich winter food used by Palearctic grouse (Salo 1973, Andreev 1988). The hazel grouse is the smallest grouse in the Palearctic boreal forest, and small species require more nutritious food than larger species (Peters 1983, Andreev 1988). This may be one important reason why hazel grouse use alder and birch as winter food.

Hazel grouse appeared to prefer catkins over buds in both alder and birch. These birds made greater use of tertiary food sources when catkins were scarce (Table VII-1) and the proportion of catkins in crops declined through winter in other studies (Donaurov 1947, Semenov-Tyan-Shanskii 1959, Salo 1971, Ahnlund & Helander 1975). Only alder and birch catkins, of the winter foods of Palearctic grouse, contain energy and protein levels close to the optimum for grouse (Andreev 1988). Foraging sites within the canopy were distributed in the same manner as the biomass of catkins and buds (Tables VII-2 & 3).

Does winter food limit numbers and/or distribution?

Hazel grouse not only showed a high preference for alder, but also selected tall trees near spruce cover. Selection of tall trees may reflect the bird's apparent preference for catkins, which, in black alder, are usually not produced until the tree is 40 years old (Tallantire 1974), when it is usually >10 m tall (McVean 1953). Selection of trees near spruce, also reported by Donaurov (1947), may provide ready access to cover, which protects them from avain predators. There are many reports of goshawks (Accipiter gentilis) attacking and killing hazel grouse as they foraged in deciduous trees in winter (Donaurov 1947, Pynnönen 1954, Semenov-Tyan-Shanskii 1959, Gavrin 1969, Chapter VI). As a result of this selection, only 34% of the alders >3 m tall were classed as preferred trees for foraging on the study area.

Territory size was correlated negatively with both alder density and, almost significantly, with population density, suggesting that territories were feeding territories and that alders were an important defended resource (Gauthier 1987, Hixon 1980). In addition, the alders in all winter territories observed during this study could have provided the required food resources for two hazel grouse. Winter territories contained, on average, 144 preferred alders, which would have had standing crops of about 5.6 kg (dry weight) catkins in 1987-88, 81.8 kg in 1988-89, 15.2 kg in 1989-90, and 60.8 kg in 1990-91, plus 31.7 kg buds each year, based on data in Table VII-2 and the catkin indices. The daily requirement of hazel grouse in winter is about 46 g of food, dry weight (Donaurov 1947, Semenov-Tyan-Shanskii 1959, Andreev 1979), and the period of arboreal feeding on the Grimsö study area was about 200 days (late September to early April), giving a requirement of about 9.2 kg (dry weight) per bird. As male and female territories usually overlapped (Chapter V), about 18.4 kg would be removed from a given territory. The amount of alder catkins on an average territory was 30% of this in 1987-88, 440% in 1988-89, 83% in 1989-90, and 325% in 1990-91. Buds comprised 172% of the food requirements within a territory each year. Thus, the alders within an average territory could provide more than enough winter nutrition each year, assuming that all buds and catkins were available to foraging grouse and were chemically acceptable (Jakubas et al. 1989). In addition, the smallest number of preferred alders observed in 20 territories was 82, which should contain about 18.0 kg buds and 3.2 to 46.6 kg catkins (based on the calculations given above), compared with a calculated minimum requirement of 18.4 kg. Moreover, there were about 14.5 birches for every alder on the study area (Table VII-1), also suggesting that the absolute amount of food within a territory was adequate every winter.

At two levels of scale above that of territory, there were positive correlations between the abundance of hazel grouse and that of alder. On a local patch scale, hazel grouse densities were higher where alder densities were also higher (Fig. VII-4). On a biogeographical scale, hazel grouse densities were correlated with densities of alder (Fig. VII-5), but not birch (Fig. VII-6). Donaurov (1947) found that winter densities of hazel grouse in spruce forests of the Ural Mountains were greater where alder, birch, rowan, and willow were also present than where only birch was present. Moreover, at two levels of scale there were also positive relationships between the distribution of hazel grouse and that of alder. On a territory scale, occupied territories had almost 10 times more preferred alders than unoccupied contiguous areas. On a landscape scale, hazel grouse distribution was positively related with alder distribution (Table VII-5).

The correlations between the abundance and distribution of hazel grouse and alder could be the result of correlation with factors other than alder occurrence, but that are correlated with alder occurrence (Table VII-4). Nevertheless, the documented strong preference for alder as winter food (Table VII-1) strongly suggested that alder was, indeed, a major factor determining the abundance and distribution of hazel grouse in Fennoscandian boreal forests. This suggestion was strengthened when compared with several other studies that failed to find consistent patterns in important habitat elements at different levels of scale (review in Wiens 1989). Size of winter territories varied with alder density and competitor density and territories contained at least the minimum number of alders to provide food for the territory holders. Thus, the availability of suitable territories was dependent upon the abundance and distribution of alder, and the availability of alder probably limits the numbers and distribution of hazel grouse territories in winter, especially if territorial behavior caused some birds to be expelled from the limited areas with winter food (Newton 1980). This seemed to be the case (Chapter IV).

The population consequences of being an alder specialist

Alder and birch provide the most nutrious food used by Palearctic grouse and the hazel grouse, as the smallest grouse in the Palearctic boreal forest, requires the most nutritious food of Palearctic grouse (Peters 1983, Andreev 1988). This may be one important reason why hazel grouse select alder as a winter food, although this study did not provide an explanation for the selection of alder over birch. Few species compete for alder (McVean 1953). Black grouse (Tetrao tetrix) may eat alder catkins in winter, but they generally avoid habitats with spruce (Seiskari 1962), which are important to hazel grouse. Thus, the amount of alder food available in autumn is a reliable indication of that available to hazel grouse throughout the winter.

Black alder, however, is relatively uncommon. It is distributed in a patchy manner both at local and landscape levels of scale, usually as small scattered clumps or linear populations along fen edges, lake and stream shores (McVean 1953, Fig. VII-2), reflecting its relatively narrow edaphic requirements, particularly of soil moisture and fertility (McVean 1953, Børset 1985, Table VII-2). Gray alder, a more northern species, is less specific in its requirements, but also occurs in a patchy manner (Tallantire 1974, Børset 1985). Consequently, hazel grouse habitats exhibit a patchy distribution within the boreal forest. Thus, they may act as "habitat islands" of varying size with differing "interisland" distances within a "sea" of less suitable or unsuitable forest. This means that hazel grouse populations often may be disjointed naturally due to the patchy nature of their habitats.

LITERATURE CITED

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson & D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.

Ahnlund, H. & B. Helander. 1975. The food of the hazel grouse (Tetrastes bonasia) in Sweden. Viltrevy 9:221-240.

Andreev, A. V. 1979. Materialy po biologii teterevinykh ptits severo-vostochnoi Sibiri v zimnii period. Pp. 27-56 in A. V. Krechmar & F. B. Chernyavskii, eds. Ptitsy cevero-voctoka Azii. Akademiya Nauk SSSR, Vladivostok. (In

Russian)

Andreev, A. V. 1988. Ecological energetics of Palaearctic Tetraonidae in relation to chemical composition and digestibility of their winter diet. Can. J. Zool. 66:1382-1388.

Anonymous. 1977. Yearbook of forest statistics. Folia Forestalia 295:1-217. (In Finnish; English summ.)

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn, Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Børset, O. 1985. Skogskjøtsel I, skogøkologi. Landbruksforlaget, Oslo. (In Norwegian)

Cederlund, G. 1981. Daily and seasonal activity pattern of roe deer in a boreal habitat. Swedish Wildl. Res. 11:314-353.

Davies, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 in J. R. Krebs & N. B. Davies, eds. Behavioural ecology--an evolutionary approach. Blackwell Sci. Publ., Oxford.

Doerr, P. D., L. B. Keith, D. H. Rusch & C. A. Fischer. 1974. Characteristics of winter feeding aggregations of ruffed grouse in Alberta. J. Wildl. Manage. 38:601-615.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika 4:77-122. (In Russian)

Fretwell, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Ecol. No. 5. Princeton Univ. Press, Princeton, New Jersey.

Gauthier, G. 1987. The adaptive significance of territorial behaviour in breeding buffleheads: a test of three hypotheses. Anim. Behav. 35:348-360.

Gavrin, V. F. 1969. Ekologiya ryabchika v Belovezhskoi Pushche. Gosudarstvennoe Zapovedno-Okhotnich'e Khozyaistvo "Belovezhskaya Pushcha" 3:146-172. (In Russian)

Gutzwiller, K. J. & S. H. Anderson. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89:534-548.

Hägglund, B. & J.-E. Lundmark. 1984. Handledning i bonitering med

Skogshögskolans boniteringssystem; del 3 markvegetationstyper, skogsmarksflora. Skogsstyrelsen, Jönsköping. (In Swedish)

Harvey, M. J. & R. W. Barbour. 1965. Home range of Microtus ochrogaster as determined by a modified minimum area method. J. Mammal. 46:398-402.

Hengeveld, R. 1987. Scales of variation: their distinction and ecological importance. Ann. Zool. Fenn. 24:195-202.

Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115:510-530.

Jacob, L. 1988. La régime alimentaire de la gelinotte des bois (Bonasa bonasia L.): synthèse bibliographique. Gibier Faune Sauvage 5:95-111.

Jakubas, W. J., G. W. Gullion & T. P. Clausen. 1989. Ruffed grouse feeding behavior and its relationship to secondary metabolites of quaking aspen flower buds. J. Chem. Ecol. 15:1899-1917.

Kenward, R. 1987. Wildlife radio tagging; equipment, field techniques and data analysis. Academic Press, London.

Lindén, H. 1983. Pyy. Pp.114-115 in K. Hyytiä, E. Kellomäki & J. Koistinen, eds. Suomen lintuatlas. SLY:n Lintutieto Oy, Helsinki. (In Finnish)

Lindén, H. & P. Rajala. 1981. Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. Finnish Game Res. 39:13-34.

Marcström, V., R. Brittas, E. Engren & T. Winqvist. 1983. Field form for description of woodland grouse habitat. Sveriges lantbruksuniversitet, Uppsala, Sweden.

Marzluff, J. M. & R. P. Balda. 1988. Resource and climatic variability: influences on sociality of two southwestern corvids. Pp. 255-283 in C. N. Slobodchikoff, ed. The ecology of social behavior. Academic Press, Inc., New York.

McVean, D. N. 1953. Biological flora of the British Isles, Alnus glutinosa (L.) Gaertn. J. Ecol. 41:447-466.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Moss, R. & I. Hanssen. 1980. Grouse nutrition. Commonwealth Bur. Nutr., Nutr. Abstr. Rev.--Ser. B. 50:555-567.

Newton, I. 1980. The role of food in limiting bird numbers. Ardea 68:11-30.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. 5:113-117.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge.

Pulliam, H. R. & G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biol. 6:169-197.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebenweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Salo, L. J. 1971. Autumn and winter diet of the hazel grouse (Tetrastes bonasia L.) in northeastern Finnish Lapland. Ann. Zool. Fenn. 8:543-546.

Salo, L. J. 1973. Chemical composition and caloric content of the autumn and winter diet of Tetrastes bonasia L. in northeastern Finnish Lapland. Ann. Zool. Fenn. 10:384-387.

Seiskari, P. 1962. On the winter ecology of the capercaillie, Tetrao urogallus, and the black grouse, Lyrurus tetrix, in Finland. Pap. Game Res. 22:1-119.

Semenov-Tyan-Shanskii, O. 1959. Ekologiya teterevinykh ptits. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1-318. (In Russian)

Stamps, J. A. & K. Tollestrup. 1984. Prospective resource defense in a territorial species. Am. Nat. 123:99-114.

Svoboda, F. G. & G. W. Gullion. 1974. Techniques for monitoring ruffed grouse food resources. Wildl. Soc. Bull. 2:195-197.

Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse Bonasa bonasia in spring and autumn. Ornis Fennica 68:in press.

Tallantire, P. A. 1974. The palaeohistory of the grey alder (Alnus incana (L.) Moench.) and black alder (A. glutinosa (L.) Gaertn.) in Fennoscandia. New Phytol. 73:529-546.

Uusvaara, O. 1963. The structure of the habitats of the hazel grouse. Suomen Riista 16:31-45. (In Finnish, English summ.)

Wiens, J. A. 1989. The ecology of bird communities. Vol. 2, processes and variations. Cambridge Univ. Press, Cambridge.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Engelwood Cliffs, N. J.

VIII. SMALL-SCALE SPATIAL HETEROGENIETY IN SURVIVAL RATES OF TERRITORIAL HAZEL GROUSE

INTRODUCTION

An understanding of spatial patterns of survival is very important to the understanding of population dynamics and the potential for natural regulation of an animal species (Wiens 1976, Lomnicki 1978, 1988, Pulliam 1988). It is also important in determining habitat quality, as habitat quality must be defined in terms of demographic parameters, with habitats varying from "sources" (net exporters of individuals) to "sinks" (net importers of individuals) (Van Horne 1983, Pulliam 1988). There is evidence suggesting that spatial heterogeniety of survival rates exists for at least some grouse, as variations in survival rates have been related to differences among habitats (Rusch & Keith 1971, Lindén & Wikman 1983), forest structure (Gullion & Marshall 1968, Boag 1976, Thompson & Fritzell 1989), and forest fragmentation (Wegge et al. 1990) and to distance from predator nests (Eng & Gullion 1962) and habitat edges (Gullion & Marshall 1968).

Lindén & Wikman (1983) found that the vulnerability of hazel grouse (Bonasa bonasia) to goshawk (Accipiter gentilis) predation varied among habitat types in Finland, but no studies exist of spatial heterogeniety of survival on a local scale. In the western Palearctic, hazel grouse select habitats with a high proportion of spruce, which has been explained as a requirement for cover from predators (Donaurov 1947, Ivanter 1962, Gavrin 1969, Eiberle & Koch 1975, Wiesner et al. 1977, Scherzinger 1979, Marcström et al. 1982). However, this has never been tested. Also, interspersion of habitat types within a small area, implying a high edge-to-area ratio, has been described as important for good quality hazel grouse habitat (Pynnönen 1954, Bergmann et al. 1982), but studies of ruffed grouse (Bonasa umbellus) have shown that survival is lower for males with territores near habitat edges (Gullion & Marshall 1968). Thus, a high edge-to-area ratio may not be as favorable as has been thought.

This study was part of an investigation of the social organization of territory-holding hazel grouse. The objectives were twofold: 1) to determine if survival varied spatially among territories on a local area and 2) if so, to determine the relationship of forest structure, including the presence of spruce and edges, to survival.

STUDY AREA

The study area was within a forest reserve (522 ha) on the Grimsö Wildlife Research Area in southcentral Sweden (59-60° N and 15-16° E). Most of the reserve burned during a fire in 1914, and very little forest management has occurred on the area since 1972. The study area (285 ha total, 195 ha of forest) encompassed the western half of the reserve. The forest was dominated by Norway spruce (Picea abies, 56% of trees), birches (Betula spp., 23%), and Scots pine (Pinus sylvestris, 15%). Where the overstory was open enough to permit it, there was an understory of young spruce trees. Although the forest fire and previous cutting created a mosaic of age classes on the study area, the species composition of the forest was quite homogeneous, dominated by spruce throughout. The surrounding forest was managed intensively, using clearcutting, thinning, and clearing of understory vegetation.

Major potential predators of the hazel grouse included the goshawk, pine marten (Martes martes), red fox (Vulpes vulpes), and stoat (Mustela erminea). On the Grimsö Wildlife Research Area, the densities per 1000 ha of major predators were ca. 0.6 breeding goshawks (Widén 1985), 0.5-2 adult red foxes in spring, and 2-4 pine martens (E. Lindström, pers. comm.). Large owls were rare.

METHODS

Hazel grouse were captured by luring or chasing them into nylon fishing nets, primarily in spring and autumn, during September 1987-September 1990. The birds were weighed to the nearest 10 g with a Pesola 500 g spring scale; net weight was determined by subtracting the estimated weight of crop contents, as determined from weighing crop contents of dead birds (Comeau & Keppie 1989). They were then marked with 16-g necklace-type transmitters (Kenward 1987). Age was determined by the coloration of the innermost primary (Stenman & Helminen 1974). Here, a bird is termed a juvenile until its first birthday. Two birds marked while still with their mothers were not included in the data set until they had established territories in the autumn, so all birds were known to be territorial. Birds were relocated three to six times per week throughout the year.

Determination of the type of predator responsible for a kill was based on whether remiges were plucked out (avian predator) or sheared off (mammalian predator), and from droppings, tracks, and tooth or beak marks on the transmitter, collar, or colored bands. The year was divided into five seasons, each nine to 13 weeks long: spring (late March to late May, weeks 13-21), summer (late May to late August, weeks 22-34), autumn (late August to early November, weeks 35-44), early winter (early November to mid-January, weeks 45-2), and late winter (mid-January to late March, weeks 3-12). These were determined a priori from a study of hazel grouse behavior at a similar latitude in Finland (Pynnönen 1954), except that winter was divided into two halves so the seasons would be of similar length.

Survival rates were estimated for seasonal and annual periods by calculating survival for weekly intervals and multiplying the weekly survival rates to obtain the rate for the desired period (Trent & Rongstad 1974). Confidence intervals of daily survival rates were obtained using the Poisson approximation (Krebs 1989). Differences in survival between sexes or birds in different areas was tested using the Gehan test (Miller 1981), a nonparametric test of survival time that is censored to account for birds alive at the end of the study. Differences in seasonal survival were tested using $\underline{X}^2$ tests, corrected for continuity when appropriate (Miller 1981).

Annual survival of hazel grouse was calculated for nine generalized territories on the study area. These generalized territories were defined by overlaying maps of the boundaries of seasonal territories for all radio-marked birds, and drawing the boundaries of the generalized territories where the actual boundaries most often occurred. This allowed a comparison of survival rates with the forest characteristics within different areas, because the generalized territories corresponded well with actual territories. Hazel grouse are year-round residents with high site philopatry between seasons (Chapter IV). The number of days each radio-marked grouse spent within each generalized territory was determined from the proportion of relocations there each month, because the generalized territories did not exactly coincide with actual territories. The birds spent an average of 79±1.7% of their time during a given season within the generalized territory they used most (N=91 bird-seasons). An annual hazel grouse survival rate was calculated for each generalized territory as the daily survival rate, based on all deaths and bird-days within the generalized territory, raised to the 365 power (Trent & Rongstad 1974).

The probable kill sites of hazel grouse were usually found, and it appeared that the predators did not carry the prey far before consuming it. Therefore, forest structure was determined within 100 m of each site where grouse were found dead, termed kill site. Forest structural category, according to the classification scheme of the Swedish Forest Service (Domänverket), was obtained from their maps (1:10,000) made in 1981. Category 2 forests are young (mean age on the reserve of 33±9.3 yr in 1989, N=4 stands), dense forests that required precommercial thinning, category 3 forests were older (60±3.5yr, N=17), more open and required commercial thinning, and category 4 forests (101±12.7yr, N=7) had lower tree stem densities and were mature enough to be harvested. The proportion of spruce among trees >3 m tall was determined from vegetation plots of 10-m radius placed systematically over the entire study area at the corners of a 70x70 m grid (2 plots per ha).

Edge was measured from a detailed orienteering map (1:15,000) that showed features not shown on the forestry map. "Very dense forest", used to determine the within-forest edge between very dense and "normal" forest, was indicated on the map as forest thick enough to making running difficult. Distances to various types of edge (dense-normal forest, forest-open bog, forest-river, forest-lake, road, and powerline) were measured to the nearest 5 m from the orienteering map for each kill site and for an equal number of randomly-located sites. Random sites were within areas used by hazel grouse.

Means are presented with standard errors of the mean. Multiple regressions and $\underline{X}^2$ tests had adequate samples sizes, based on the criteria in Zar (1974). Null hypotheses were rejected at a 5% probability level.

RESULTS

Survival data, based on radio telemetry, were obtained from 26 hazel grouse (8089 radio-days), 13 males (5252 radio-days) and 13 females (2837 radio-days). All but four birds were recaptured to replace transmitters before battery failure. These four were recaptured after battery failure and the transmitters were replaced, thus the fate of all marked grouse was known until the study was terminated on 28 September 1990, when three were still alive.

The predator causing the death of two additonal hazel grouse was determined for a bird marked with a backpack transmitter and an unmarked bird. At any given time, 33-100% of the females and 60-100% of the males on the study area were marked.

Effects of the transmitters

It is always difficult to determine if transmitters affect survival. I sometimes heard a slapping noise when the radio-marked birds flew, probably the wings hitting the antenna. Transmitter weight did not appear to be a major problem, because survival time in days following marking for birds that had borne only one transmitter was not correlated with transmitter weight, as a proportion of the net weight of the bird ($r^2=0.01$, df=11, $P=0.74$). Transmitters weighed on average 4.4±0.1% of the birds' net weight, adjusted for crop contents ($N=49$, range 3.4-5.3%).

The predators

The proximate cause of all recorded mortality was apparent predation. The probable predators for 25 kills were: 15 (60%) avian predators (probably all goshawks), and 10 (40%) mammalian predators (primarily marten, but possibly also fox and stoat).

Seasonal and sexual variation in survival rates

On an annual basis, the observed survival rate was 0.48 for males, 0.19 for females, and 0.36 for all birds combined. There was no significant difference between males and females in survival time following marking (Gehan test, $U=49$, df=25, $P=0.28$), although this may have been a consequence of small sample sizes. Also, no significant differences were found in seasonal survival rates within either sex or for sexes combined (Table VIII-1). With the data available, it was not possible to determine if avian and mammalian predation differed by season.

Spatial pattern of survival

Annual survival rates of hazel grouse varied considerably and significantly among generalized territories (0.083-1.000,Table VIII-2). Survival rates were higher within generalized territories in the northern part of the study area (Fig. VIII-1). This difference was significant, as a grouse with a territory in the northern part (generalized territories A-E) survived on average more than 1.4 years following capture (503±103 days, $N=9$, including 3 grouse still alive at the end of the study), compared to 0.6 years in the southern part (generalized territories F-I, 203±58 days, $N=14$, Gehan test, $U=75$, df=22, $P=0.018$). One of the grouse alive at the end of the study was resighted in the northern part of the area seven months later, in May 1991. The survival of marked birds was consistently higher during each season in the northern part of the study area, but the difference was only significant in early winter (Table VIII-3).

Hazel grouse on the northern part of the area were mostly adults (75%, $N=12$). Fewer adults were found in the southern area (53%, $N=15$), but not

Table VIII-1. Seasonal survival rates of radio-marked male and female hazel grouse on a forest reserve (C.I. = confidence interval).

		Season				
Sex	Variable	Spring	Summer	Autumn	Early winter	Late winter
Male	Daily rate	0.9989	0.9971	0.9990	0.9937	0.9978
	95% CI	0.9999-	0.9990-	0.9999-	0.9992-	0.9996-
		0.9948	0.9934	0.9952	0.9929	0.9930
	Seasonal rate	0.945	0.768	0.934	0.934	0.854
	N (days)	903	1388	974	1093	900
Female	Daily rate	0.9929	0.9968	0.9984	0.9958	0.9974
	95% CI	0.9994-	0.9991-	0.9999-	0.9992-	0.9999-
		0.9818	0.9917	0.9923	0.9868	0.9876
	Seasonal rate	0.605	0.741	0.894	0.576	0.826
	N (days)	422	928	613	473	380
Both	Daily rate	0.9970	0.9970	0.9987	0.9987	0.9977
	95% CI	0.9990-	0.9986-	0.9998-	0.9987-	0.9994-
		0.9931	0.9942	0.9960	0.9933	0.9940
	Seasonal rate	0.817	0.761	0.917	0.735	0.847
	N (days)	1325	2316	1587	1566	1280

Table VIII-2. Annual survival rates of territorial hazel grouse in nine generalized territories within the study area (C.I.= confidence interval).

Generalized territory	N birds[a]	Transmitter Days	Deaths	Annual survival Rate[b]	Annual survival 95% CI
A	6	880	0	1.000	
B	7	1229	3	0.416	0.099-0.783
C	9	1162	0	1.000	
D	8	318	0	1.000	
E	9	963	2	0.464	0.092-0.874
F	12	443	3	0.083	0.006-0.499
G	11	1119	5	0.193	0.033-0.518
H	14	1048	7	0.086	0.009-0.322
I	9	319	0	1.000	

[a] Number of radio-marked birds recorded in the territory.

[b] $[(\text{Transmitter days} - \text{deaths}) \div \text{transmitter days}]^{365}$.

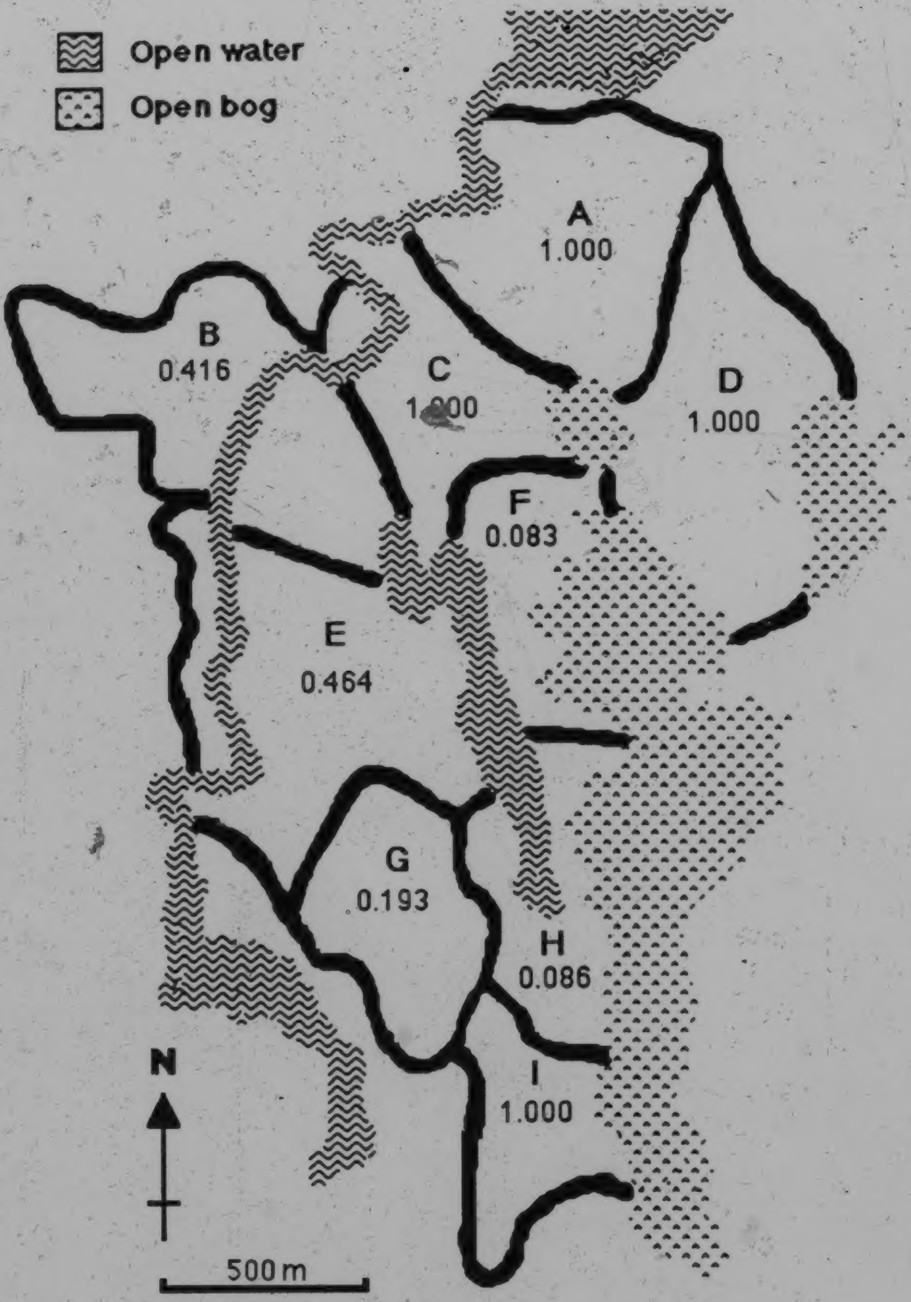

Fig. VIII-1. Map of the study area, indicating annual survival rates of territorial hazel grouse within the nine generalized territories.

Table VIII-3. Seasonal survival of hazel grouse in the northern part (generalized territories A-E) and southern part (F-I) of the study area.

	Northern area		Southern area		Difference	
Season	N	% surviving	N	% surviving	χ^2_c	P
Spring	18	89	12	83	0.01	0.92
Summer	17	88	12	58	2.00	0.16
Autumn	12	100	14	86	0.39	0.53
Early winter	12	100	15	53	5.32	0.02*
Late winter	12	92	8	75	0.15	0.70

significantly so (χ^2_c=0.57, df=1, P=0.45). Included in this data set were radio-marked grouse (age when first captured), one grouse that died the day of capture (capture stress?), and an unmarked grouse found dead; both birds marked as chicks were excluded.

Occurrence of kill sites in relation to forest structure

Kill sites on the study area (20 radio-marked birds and one unmarked bird; four kills occurred outside the described area) were found more than expected in category 2 forest (one group χ^2=39.5, df=2, P<0.0001, Table VIII-4). The distribution of birds killed by avian versus mammalian predators did not differ by forest category (χ^2_c= 0.03, df=1, P=0.87, categories 3 and 4 combined).

Spruce has been considered to be important for hazel grouse as cover from predators. The areas surrounding kill sites on the study area had a lower percentage of spruce trees (51±0.7%, N=20) than similar-sized areas within the area as a whole (56%, Wilcoxon sign-ranked test, df=19, P=0.0002).

Kill sites were closer to edges, including forest-water edge (lake or river), the edge of very dense-normal density forest, and the closest edge, than were random sites (Table VIII-5). Again, there were no significant differences between kill sites of avian and mammalian predators (Mann-Whitney U tests, P values varied from 0.55 to 0.98). Type of closest edge varied significantly between kill sites and random sites (χ^2=14.2, df=2, P=0.0008). Edge between very dense and normal forest was most commonly the closest to kill sites, whereas edge to an open bog was for the random sites (closest edge to kill sites and random points, respectively, was: dense-normal forest edge, 54 and 8%; open bog edge, 25 and 75%; lake or river edge, 13 and 4%; and road or powerline edge, 8 and 13%; N=24 for both categories).

Hazel grouse survival rates and forest characteristics of generalized territories

To examine the relationship between forest structure and survival at a higher scale, the annual survival rates of hazel grouse in the generalized territories was compared with the factors found to be important at the kill-site level: proportion of category 2 forest, density of combined edges of very dense-normal forest and forest-water, and proportion of spruce trees within the territory. One-tailed tests were used here, because the results of the tests at the kill-site level led me to expect the direction of the relationships. A multiple stepwise regression showed that only one of these variables, the proportion of category 2 forest, arcsine transformed, was sufficient to explain 94% of the variation in hazel grouse survival (also transformed) among generalized territories (r^2=0.945, df=7, F=121.28, P<0.0005, Fig. VIII-2). Including the other two factors into a multiple regression had almost no effect (r^2=0.946). It can be difficult to interpret the results when survival in four of the generalized territories was 100% (Table VIII-2). Of course, true survival of hazel grouse is not 100% in any territory, and a measured survival of 100% can be an artifact of inadequate sampling effort. However, the relationship between distribution of kill sites and forest age category was not an artifact of the distribution of sampling effort in this

Table VIII-4. Distribution of sites where hazel grouse were found dead in relation to forest structural categories on the forest reserve.

Forest structural category	Percent of			
	Area[a]	All kills[a] (N=21)	Avian kills (N=14)	Mammalian kills (N=7)
2 (young forest)	16	67	71	57
3 (mid-aged forest)	54	24	21	29
4 (mature forest)	30	10	7	14

[a] Only within hazel grouse generalized territories.

Table VIII-5. Distribution of 24 hazel grouse kills and 24 random points in relation to distance (in m) from various edges.

Edge type	Kill sites		Random sites		Mann-Whitney U value	P value
	Mean	SE	Mean	SE		
Dense-normal forest	70	12.9	241	44.1	133	0.001*
Lake/river	205	42.3	368	49.9	155	0.006*
Open bog	96	15.2	73	11.0	247	0.40
Powerline	390	74.4	491	82.0	254	0.48
Road	435	71.8	529	82.6	263.5	0.61
Closest edge	37	8.5	62	11.3	193	0.049*

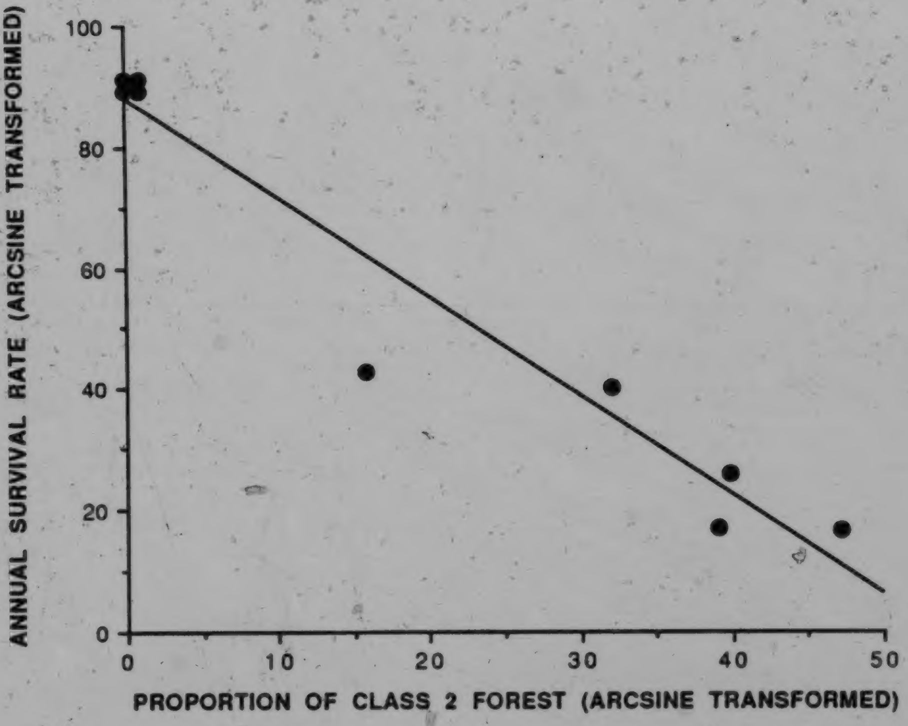

Fig. VIII-2. Relationship between the annual survival rate of territorial hazel grouse and proportion of category 2 forest (both arcsine transformed) in the generalized territories on the study area ($r^2=0.945$, df=7, $P<0.0005$).

case. Effort occurred evenly across groups of generalized territories: 2679 bird-days in territories with no category 2 forest, 2192 days in those with 7-29%, and 2610 days in those with 39-54%. However, the number of birds killed was higher than expected, based on the number of bird-days, in areas with more young forest: 0 kills in territories with no category 2 forest, 5 in those with an intermediate proportion, and 15 in those with a high proportion of category 2 forest (one group $\chi^2=16.5$, df=2, P=0.0003).

Density of the combined edge of very dense-normal forest and forest-water was negatively related to survival, arcsine transformed ($r^2=0.614$, df=7, P=0.006) and proportion of spruce within the territory, arcsine transformed, was positively related to survival, also transformed ($r^2=0.547$, df=7, P=0.01). However, both of these factors were significantly correlated with the transformed proportion of category 2 forest (r=0.822, df=7, P=0.007 and r=0.745, df=7, P=0.02, respectively). Therefore, although they may have had an effect on survival, it could not be distinguished from that of proportion of category 2 forest alone.

Alder (Alnus glutinosa and A. incana) provides the most important winter food for hazel grouse in this area (Chapter VII). The density of alders >10 m high and ≤15 m from spruce forest (preferred trees for foraging) was not correlated with the transformed annual survival of hazel grouse in generalized territories ($r^2=0.346$, df=6, P=0.13). Generalized territory D (Fig. VIII-1) was excluded from this test because hazel grouse were not observed to overwinter there.

DISCUSSION

Spatial heterogeniety of survival rates

Annual survival of hazel grouse varied dramatically over short distances. The most important factor related to survival appeared to be forest structure. This factor was significant at two levels of scale, both at kill sites and at the generalized territory level. At the territory level of scale, the variation in this factor explained 96% of the variation in annual survival rates. I conclude that forest structure within the territory was the most important factor, of those measured, influencing the likelihood of survival for territorial hazel grouse and for shaping the spatial heterogeniety of survival rates found on this study area. The density of edges and proportion of spruce also may have influenced survival, but probably to a lesser degree.

Category 4 forests within the forest reserve were different from those in managed forests. With no forest management within the reserve for ca. 20 years, young spruce were present, giving the forest a two-layered structure in many areas. The cover provided by these young spruce may be important, as hazel grouse immediately seek thick cover when alarmed (Scherzinger 1979). Outside the reserve, these forests had been thinned and cleared of undergrowth, giving them an open, single-layered structure. In fact, hazel grouse avoided older managed forest at Grimsö (Angelstam & Swenson, in prep.). This suggests that the presence of an understory of young spruce, giving a forest a layered structure, is a key requirement for secure hazel grouse habitat, as suggested by Eiberle & Koch (1975) and Wiesner et al. (1977). This is similar to the situation for the closely related ruffed grouse in Nearctic boreal forests. There, survival is much higher in young pine or all spruce and fir (Abies sp.) forests than in older, single-layered pine forests lacking a coniferous understory (Gullion & Marshall 1968). The occurrence of spruce was found to be less important for survival in my study than expected, based on the literature. This was probably because spruce was the dominant tree throughout the study area. The coefficient of variation in mean proportion of spruce trees within the generalized territories was only 10.2%.

The difference in survival rates between the more and less secure parts of the study area was greatest in early winter. All seven kills recorded in this season occurred during a 40-day period, from 8 November to 18 December. This was following leaf fall (normally completed around 20 October), when hazel grouse were feeding arboreally, after thrushes and other migratory alternative prey species had left, and when a considerable influx of juvenile goshawks arrived in this part of Sweden (Höglund 1964). Moreover, the capture rate of goshawks and proportion of juveniles among goshawks captured on the Grimsö area were both higher in September through November than from December through February (Widén 1985).

My results were consistent with those of Lindén and Wikman (1983), although we studied spatial heterogeneity of survival at different levels of scale. They studied a fluctuating hazel grouse population and a goshawk population at the landscape scale, recording changes in density by habitat types over a 500 km^2 area in southern Finland. When hazel grouse were abundant, they were distributed more evenly among the available habitats than during population lows, when the birds were concentrated in preferred habitats, and distribution became patchy. Moreover, the number of hazel grouse killed per goshawk during the breeding season was positively and exponentially correlated with adult hazel grouse density. Thus, they concluded that the patchy distribution of hazel grouse habitat acts to stabilize predation, because hazel grouse "escape" to the shelter of secure habitats during population lows. My study was at a local scale (195 ha of forest); I recorded survival rates on contiguous territories with much smaller differences in habitat types. Even so, the forest environment appeared to be very heterogeneous with respect to the security of hazel grouse habitat even within spruce-dominated forests.

Spatial heterogeneity of habitat quality is probably a general phenomenon in hazel grouse habitats. Not only do survival rates vary among habitat types (Lindén & Wikman 1983) and with forest structure within a habitat type (this study), but alder, the major winter food plant and highly correlated with the abundance and distribution of hazel grouse, is relatively uncommon and also is distributed in a patchy manner (Chapter VII). Survival varied independently of alder density in this study. This could explain why hazel grouse are often distributed in a patchy manner in forests (Bergmann, et al. 1982).

Hazel grouse survival and habitat selection by the predators

The goshawk was the most important predator on the study area, followed by the pine marten. This is typical throughout the range of hazel grouse, with the sable (Martes zibellina), replacing the marten in the eastern Palearctic (Bergmann et al. 1982). Interestingly, the cause of death of hazel grouse on the study area (60% goshawks, 40% mammals) was similar to that found for black grouse (Tetrao tetrix) at Grimsö (58% goshawks, 38% mammals, Angelstam 1984). However, the fox was the major mammalian predator of black grouse.

Survival rates of hazel grouse were related to forest structure. Forest category 2 was the least secure type of forest, whereas category 4 was the most secure (Table VIII-4). Both the goshawk and the pine marten select category 4 forests and avoid category 2 forests at Grimsö (Widén 1989, Storch et al. in press). Goshawks showed no preference for either spruce or pine forests (Widén 1989), but in southeastern Norway, pine marten preferred to hunt in spruce forests in winter (Wabakken 1985). At Grimsö, grouse are a relatively important part of the diet of goshawks, but not of martens (Widén 1987, Storch et al. in press). The higher survival of hazel grouse in habitats preferred by the major predators underlined the survival value of category 4 spruce forests to hazel grouse. However, the studies of goshawks and marten were made on the entire Grimsö area, which is dominated by managed forests, where category 4 forest has a very open understory as a result of thinning and clearing. Raptors often prefer to hunt in more open habitats, where foraging is more profitable even if prey densities are lower (Preston 1990).

Effect of transmitters on survival

No measurable effects of the weight of transmitters on survival were found in this study. Also, the annual survival rate found in this study, 0.36, was higher than previous estimates, 0.23 based on band recoveries (Gaidar 1973) and 0.30 based on annual transect surveys (Wikman 1977). However, necklace-type transmitters have been suggested to reduce the survival rates of sharp-tailed grouse (Tympanuchus phasianellus) by interfering with their ability to fly (Marks & Marks 1987), perhaps because the wings slap against the antennas, as I also noted. It was clear that, in my study, the transmitters did not have the dramatic effects on survival reported by Marks & Marks (1987). It is possible, however, that the transmitters increased the vulnerability of some hazel grouse to predators, such as heavy, gravid females in spring and both sexes in winter when crop contents are heavy, up to 50 g (Donaurov 1947). Even if this were the case, this would not have affected the conclusions about spatial variation in survival, the main subject of this study.

LITERATURE CITED

Angelstam, P. 1984. Sexual and seasonal differences in mortality of the black grouse Tetrao tetrix in boreal Sweden. Ornis Scand. 15:123-134.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn, Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Boag, D. A. 1976. Influence of changing grouse densities and forest attributes on the occupancy of a series of potential territories by male ruffed grouse. Can. J. Zool. 54:1727-1736.

Comeau, R. M. & D. M. Keppie. 1989. Crop weights used to adjust body weights of live spruce grouse. J. Wildl. Manage. 53:818-819.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Zapovednika 4: 77-122. (In Russian)

Eiberle, K. & N. Koch. 1975. Die Bedeutung der Waldstruktur für die Erhaltung des Haselhuhnes (Testrastes bonasia L.). Sweiz. Z. Forstw. 126:876-888.

Eng, R. L. & G. W. Gullion. 1962. The predation of goshawks upon ruffed grouse on the Cloquet Forest Research Center, Minnesota. Wilson Bull. 74:227-242.

Gaidar, A. A. 1973. Ringing of Tetrastes bonasia L. and its results. Byulleten´ Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii 78(6):120-124. (In Russian, English summ.)

Gavrin, V. F. 1969. Ekologiya ryabchika v Belovezhskoi Pushche. Gosudarstvennoe Zapovedno-Okhotnich´e Khozyaistvo "Belovezhskaya Pyshcha" 3:146-172. (In Russian)

Gullion, G.W. & W. H. Marshall. 1968. Survival of ruffed grouse in a boreal forest. Living Bird 7:117-167.

Höglund, N. H. 1964. Der Habicht Accipiter gentilis Linné in Fennoskandia. Viltrevy 2:195-270.

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In Russian)

Kenward, R. E. 1987. Wildlife radio tagging; equipment, field techniques and data analysis. Academic Press, London.

Krebs, C. J. 1989. Ecological methology. Harper & Row, Publ., New York.

Lindén, H. & M. Wikman. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. J. Anim. Ecol. 52:953-968.

Lomnicki, A. 1978. Individual differences between animals and natural regulation of their numbers. J. Anim. Ecol. 47:461-475.

Lomnicki, A. 1988. Population ecology of individuals. Princeton Univ. Press, Princeton, New Jersey.

Marcström, V., R. Brittas & E. Engren. 1982. Habitat use by tetraonids during summer--a pilot study. Proc. Intern. Grouse Symp. 2:148-153.

Marks, J. S. & V. S. Marks. 1987. Influence of radio collars on survival of sharp-tailed grouse. J. Wildl. Manage. 51:468-471.

Miller, R. G., Jr. 1981. Survival analysis. John Wiley & Sons, New York.

Preston, C. R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor 92:107-112.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652-661.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Rusch, D. H. & L. B. Keith. 1971. Ruffed grouse--vegetation relationships in central Alberta. J. Wildl. Manage. 35:417-429.

Scherzinger, W. 1979. Zum Feindverhalten des Haselhuhnes (Bonasa bonasia). Vogelwelt 100:205-217.

Stenman, O. & M. Helminen. 1974. Aging method for hazel grouse (Tetrastes bonasia) based on wings. Suomen Riista 25:90-96. (In Finnish, English summ.)

Storch, I., E. Lindström & J. de Jounge. In press. Diet and habitat selection of the pine marten in relation to competition with the red fox. Acta Theriol.

Thompson, F. R. & E. K. Fritzell. 1989. Habitat differences between perennial and transient drumming sites of ruffed grouse. J. Wildl. Manage. 53:820-823.

Trent, T. T. & O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459-472.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Wabakken, P. 1985. Vinternæring, habitatbruk og jaktatferd hos mår (Martes martes) i sørøst-norsk barskog. Unpubl. Thesis, Univ. Oslo. (In Norwegian)

Wegge, P., I. Gjerde, L. Kastdalen, J. Rolstad & T. Storaas. 1990. Does forest fragmentation increase the mortality rate of capercaillie? Trans. Congr. Int. Union Game Biol. 19:448-453.

Widén, P. 1985. Breeding and movements of goshawks in boreal forests in Sweden. Holarc. Ecol. 8:273-279.

Widén, P. 1987. Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. Holarct. Ecol. 10:104-109.

Widén, P. 1989. The hunting habitats of goshawks Accipiter gentilis in boreal forests of central Sweden. Ibis 131:205-231.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.

Wiesner, J., H.-H. Bergmann, S. Klaus & F. Müller. 1977. Siedlungsdichte und Habitatstruktur des Haselhuhns (Bonasia bonasa) im Waldgebiet von Bialowieza (Polen). J. Ornithol. 118:1-20.

Wikman, M. 1977. Duvhökspredation på skogsfågel i sydvästra Finland 1975-76. Viltrapport 5:59-72. (In Swedish)

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

IX. THESIS DISCUSSION

Davies & Krebs (1978) define social organization by referring to the following characteristics of a species: breeding and feeding group size (e.g. solitary, flocking); spatial organization (e.g. territorial, overlapping ranges); and mating system (e.g. monogamy, polygyny). It is now widely accepted that ecological variables impose limits on the range of types of social organization that will be adaptive, determined by the relative costs and benefits of different forms of social organization to individuals, and that many aspects of an animal's social organization can be predicted on the basis of an understanding of a limited set of environmental variables (Emlen & Oring 1977, Gosling & Petrie 1981, Pulliam & Millikan 1982). This leads to the prediction that individuals of the same species, even those in close spatial proximity, may face different environmental conditions and therefore may exhibit different social organizations (Marzluff & Balda 1988). The objectives of this study were: 1) to document the social organization of hazel grouse (Bonasa bonasia), 2) to identify ecological constraints that are important in shaping and maintaining it, and 3) to examine the ramifications of these ecological constraints and resulting social organization in terms of the potential for population regulation through intrinsic factors and other aspects of the species' ecology. I studied variability in social organization and ecological variables on both a local scale and between two study areas.

SOCIAL ORGANIZATION IN HAZEL GROUSE

Territoriality

An important characteristic of hazel grouse social organization is intrasexual territorial behavior during most of the year (Chapters III & IV). Only during summer is this behavior relaxed to a degree that hazel grouse can not be considered territorial. The territorial behavior of males had been described earlier (Pynnönen 1954, Ivanter 1962, Klaus et al. 1975, Scherzinger 1981, Bergmann et al. 1982), but I was able to document it for females also. Female territorial behavior resembles that of males, but is less obvious. On the study area, and apparently throughout most of the species' range, hazel grouse are territorial from early autumn through late spring. Juvenile hazel grouse establish territories in autumn shortly after dispersing from their broods, but several weeks after adults have reestablished their territories.

The hazel grouse is apparently the most territorial of the grouse. The red grouse (Lagopus lagopus scoticus) is probably the second most territorial grouse, but it only defends autumn territories in the early morning and, during snowy periods, they leave their territories and form flocks (Jenkins et al 1963, Watson & Jenkins 1964). Both male and female hazel grouse maintain their territories throughout the autumn and winter (Chapter IV).

The social organization of hazel grouse is variable, as would be expected if it varies with ecological factors (Marzluff & Balda 1988). In some open habitats, expecially riparian deciduous forests, hazel grouse are not territorial but form flocks in autumn and winter. Flock size varied with the openness of the habitat (Chapter VI). Even in these areas, hazel grouse are territorial in the spring, after the needles and leaves appear in the spring and provide the birds with cover.

Relationships between Individuals

Where they are territorial, hazel grouse defend territories from members of the same sex, thus providing the opportunity for a male and a female to share the same space. Since they do this, the basic social unit of hazel grouse is a pair; a male and female are found together more often than expected by chance during every season, except that the male did not spend more time with a female and her brood than was expected based on chance (Chapter V). However, during autumn and winter, the male and female do not share the same space, as their territories also overlap with those of neighboring birds of the opposite sex (Chapter V). At this time the pair bond is not an exclusive relationship. In the spring, the members of the pair do defend the same space (Chapter II).

Although the social unit is the pair, the male and female are not always together; they were within 20 m of each other during only 19-37% of the simultaneous locations, depending on the season (Chapters II & V). Birds behaved differently when alone. For example, single hazel grouse foraging in deciduous trees in winter were closer to spruce cover, used foraging sites with more canopy cover, and foraged more slowly than when foraging as a pair (Chapter V & VI).

Where hazel grouse overwintered in flocks, the flocks appeared to be distinct social units. Flocks were sexually mixed, in contrast to the sexually segregated flocking found in many grouse (Hines 1986). There was some suggestion of a hierarchial system within the flocks, which was supported by observations of captive birds (Sugimoto 1986).

Mating system

Although the social unit of hazel grouse was monogamous, a male and female together as a pair, the mating system was better described as occuring on the continuum of mating systems close to monogamy, but potentially tending towards polyandry (Chapter II). Sedentary, territorial females, synchronous nesting, and a male-biased sex ratio appeared to restrict most males to mating monogamously, but many females had the opportunity to mate polyandrously. The potential for polyandry varied spatially within the study area (depending on habitat security), varied temporally (depending on population density from year to year), and probably varied spatially within a landscape (depending on whether the habitat patch was large enough for more than one pair) (Chapter III).

This is the first study to provide evidence that challenges the widely-held belief that hazel grouse are monogamous, i.e. mate exclusively (Donaurov 1947, Pynnönen 1954, Ivanter 1962, Dement'ev et al. 1967, Hjorth 1970, Glutz von Blotzheim et al. 1973, Scherziner 1981, Bergmann et al. 1982). This is apparently also the first suggestion that a grouse species may tend towards polyandry in its mating system. This subject certainly warrants further investigation.

IMPORTANT ECOLOGICAL CONSTRAINTS

Body size

The hazel grouse is one of the smallest grouse species. Body size is included here because it has many important ecological implications (Peters 1983, Sæther & Andersen 1988). There are costs associated with being small, as small animals generally require food that is relatively more nutritious than larger species, they have smaller endogenous nutrient reserves, they have higher costs of reproduction, and they have higher mortality rates (Peters 1983, Calder 1984, Andreev 1988). There are also benefits. For example, smaller species require less food per individual and less space than larger species (Peters 1983), and they can maneuver in denser vegetation (Winkler & Leisler 1985). Hazel grouse habitat is characterized by extremely dense vegetation that is avoided by the sympatric capercaillie (Tetrao urogallus) and black grouse (T. tetrix), perhaps because they cannot maneuver well in the dense vegetation (Seiskari 1962, Rolstad & Wegge 1987). This is one factor in the niche segregation of these three species. Generally in forest grouse, small size is associated with dense habitats (Jönsson et al. 1991). Thus, the small size of hazel grouse and the dense habitats it inhabits are probably interrelated.

Abundance and dispersion of food

As stated above, small animals require relatively nutritious food. Hazel grouse forage on catkins and buds of alder and birch in the Fennoscandian boreal forest, but they prefer alder, and particularly alder catkins (Chapter VII). Alder and birch catkins provide the most protein-rich winter food used by Palearctic grouse (Andreev 1988). Although alder provides a nutritious winter food, it is relatively uncommon in the boreal forest and is patchily distributed. The data from four spatial levels of scale all indicated that alder was an important defended resource during winter and that the distribution and abundance of alder determined the distribution and abundance of hazel grouse (Chapter VII). In this respect hazel grouse differed from most other grouse, which forage on a food plant that is either dominant, or at least abundant, within the winter habitat (Doerr et al. 1974, Moss & Hanssen 1980).

In spring, nutritious food, especially newly-sprouting forbs, appeared to be an important defended resource for the females, but not for the males (Chapter III). This resource was also relatively uncommon, and was probably important for reproduction because hazel grouse have few endogenous reserves and must obtain most of the nutrients for their relatively large clutch from their spring territory (Chapter III).

Thus, in autumn, winter, and spring, it appeared that limited nutritious food resources were defended. This was probably a major factor promoting territoriality in the species (Chapter III, IV, & VII). The most important winter and spring foods coincided spatially on rich soils (Chapter VII). This may have promoted the site philopatry exhibited by territorial birds (Chapter IV). In both of the most territorial grouse species, hazel grouse and red grouse, the important winter and spring foods coincide spatially. Thus, prospecitve resource defence (Stamps & Tollestrup) may be a factor promoting this strong territoriality in some species of grouse.

During summer, the primary foods were the berries of bilberry (Vaccinium myrtillus) and cowberry (V. vitis-idaea) (Ahnlund & Helander 1975); both were very common on the area. Also during this time, there was very little territorial behavior. In addition, in Siberia, where hazel grouse were not territorial during the winter, winter food was many times more abundant and was more evenly dispersed throughout the winter habitat than in Sweden, where the hazel grouse were territorial (Chapter VI).

Predation

The major predators of hazel grouse were the goshawk (Accipiter gentilis) and pine marten (Martes martes) (Chapter VIII). Whereas defense of limited food resources appeared to be the force that separated hazel grouse into their respective territories, danger of predation apppeared to be the major force promoting gregariousness. Thus, in the Swedish study area, pairs in winter foraged farther from spruce cover, in more open sites, and could forage faster than singles (Chapters V & VI). Singles may have selected denser cover because the increased sounds of two foraging hazel grouse could provide more attraction to predators at a foraging site that also provided concealment to the predator (Chapter V). In the dense spruce forests of the Swedish study area, the intrasexual territoriality and male-female social unit may have been a compromise between the need to defend a limited food resource and the need to have a second bird for increased vigilance while foraging in deciduous trees. In the open forests of the Siberian study area, food did not appear to be a limiting factor, but there was little cover. There, the hazel grouse were faced with different ecological constraints. It did not appear to be necessary to defend food, but vigilance against predators in the more open forests appeared to be most important; the result was flocking behavior in winter (Chapter VI).

In spring, the most important factor promoting the pair bond appeared to be sentry behavior contributed by the male for the female. The female appeared to forage intensively to obtain nutrients for the formation of the clutch (Chapter III). The female increased 25% in weight during the prelaying period. An average clutch weighed 36% of a female's body weight in early spring. This was also a dangerous period for the female. Apparently the female was stressed for time and energy during this period and benefited from the sentry behavior of the male. This also was suggested by the correlation between intrapair distance and habitat security (Chapter III). One consequence of this was that females were probably more often monogamous in more dangerous habitats.

Scherzinger (1979, 1981) considered predator avoidance to be a major factor shaping hazel grouse behavior and the quiet nature of intrapair communication. In addition, hazel grouse song has cryptic properties in dense coniferous forest (Bergmann et al. 1975, Hjorth 1976). My results suggested that predator avoidance is an important factor promoting the pair as a social unit in dense habitats and the flock as a social unit in open winter habitats.

ECOLOGICAL RAMIFICATIONS

Population regulation

The territorial behavior in autumn appeared to cause the spacing of hazel grouse throughout the habitat (Chapter IV). Adults established their territories several weeks prior to the juveniles and, although the sample size was small, juvenile grouse appeared to obtain territories with less alder than adults. The amount and distribution of alder, the preferred winter food, varied greatly within the boreal forest landscape, but all winter territories contained alder, at least enough for the minimum needs of a pair of grouse (Chapter VII). Another factor that varied within the forest, but independently of alder occurrence, was the structure of the spruce forest. Following leaf fall, there was a high mortality of hazel grouse that had established territories within areas of single-layered forest (Chapter VIII). The consequence of this was that the size of the hazel grouse population appeared to be regulated in late autumn-early winter (Chapter IV). Social behavior, territorial defense of winter food, was apparently the ultimate factor in this regulation, but the proximate factor was predation in insecure habitats. Apparently, the size of a hazel grouse population would be limited by the amount of secure, two-layered spruce forest that contained enough alder to support winter territories. The hazel grouse appeared to fit Lomnicki's (1978) model of intrinsic population regulation based on spatial and temporal heterogeneity of natural environments and unequal resource partitioning among individuals (Chapter IV).

This type of population regulation was apparently characteristic of dense habitats, as evidence for it was also available from Belorussia and France (Chapter IV). In the open Siberian forests, flocks formed in winter, so population regulation did not occur in autumn (Chapter VI). There was an indication that juvenile birds were also at a disadvantage there, as they apparently had a higher mortality rate. This may have been due to a hierarchial dominance structure in the flocks, with juveniles occupying more vulnerable sites (Chapter VI).

Spatial dispersion of habitats

The winter and spring foods of hazel grouse require rich soils. In addition, alder requires wet soils. In the boreal coniferous forest, rich soils are rather rare and are often patchily distributed, so hazel grouse foods are distributed in a clumped manner on both local and landscape levels (Chapter III & VII). This situation has been intensified by man, by clearing and cultivating the best soils. As a consequence, hazel grouse habitat often consists of small patches, which are dispersed in a clumped manner throughout the landscape. Imposed upon this pattern is the heterogeniety of survival rates, resulting from variations in forest structure (Chapter VIII). This patchiness and habitat heterogeniety can have important consequences for the population dynamics of hazel grouse and how they are able to exploit suitable habitats within the landscape (Wiens 1976).

Evolution of grouse mating systems

A model was presented to explain the variation in mating systems found among the grouse. It was based on the cost of egg production for the females and their vulnerability to predation in spring (Chapter III). The smallest females have the highest costs in relation to body size, both in terms of energetic and nutrient costs of egg production, but also reduced survival, because they appear to be most time limited as they forage actively in spring. The smallest females also have the smallest endogenous nutrient reserves, on a relative basis. Thus, they must defend rich sources of nutrients and they benefit from a male as a sentry. Medium-sized females in forested habitats also may defend food resources, although the degree of territoriality declines with body size, but they do not require a male as a sentry, perhaps because the forest provides sufficient cover, and they are less stressed for time than the small females. Medium- and large-sized females in open habitats do not defend territories, but they form flocks for vigilance against predators. These flocks break up after mating and the females disperse. Male breeding behavior appears to be largely a response to these different dispersion patterns of females at the time of mating.

LITERATURE CITED

Ahnlund, H. & B. Helander. 1975. The food of hazel grouse (Tetrastes bonasia L.) in Sweden. Viltrevy 9:221-240.

Andreev, A. V. 1988. Ecological energetics of Palaearctic Tetraonidae in relation to chemical composition and digestibility of their winter diets. Can. J. Zool. 66:1382-1388.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1975. Individualität und Artspezifität in den Gesangstrophen einer Population des Haselhuhns (Bonasa bonasia L., Tetraoninae, Phasianidae). Behaviour 55:94-114.

Bergmann, H.-H., S. Klaus, F. Müller & J. Wiesner. 1982. Das Haselhuhn Bonasa bonasia, 2. Auflage. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Calder, W. A. III. 1984. Size, function and life history. Harvard Univ. Press, Cambridge, Massachusetts.

Davies, N. B. & J. R. Krebs. 1978. Introduction: ecology, natural selection and social behaviour. Pp. 1-18 in J. R. Krebs & N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford.

Dement'ev, G. P., N. A. Gladkov, Yu. A. Isakov, N. N. Kartashev, S. V. Kirikov, A. V. Mikheev & E. S. Ptushenko. 1967. Birds of the Soviet Union, Vol. IV. U.S. Dep. Inter. & Nat. Sci. Found., Washington, D.C.

Doerr, P. D., L. B. Keith, D. H. Rusch & C. A. Fischer. 1974. Characteristics of winter feeding aggregations of ruffed grouse in Alberta. J. Wildl. Manage. 38:601-615.

Donaurov, S. S. 1947. Ryabchik v Pechoro-Ilychskom zapovednike. Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika 4:77-122. (In Russian)

Emlen, S. T. & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Glutz von Blotzheim, U. N., K. M. Bauer & E. Bezzel. 1973. Handbuch der Vögel Mitteleuropas. Band 5, Galliformes und Gruiformes. Akademische Verlagsgesellschaft, Frankfurt am Main.

Gosling, L. M. & M. Petrie. 1981. The economics of social organization. Pp. 315-382 in C. R. Townsend & P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Hines, J. E. 1986. Social organization, movements, and home ranges of blue grouse in fall and winter. Wilson Bull. 98:419-432.

Hjorth, I. 1970. Reproductive behaviour in Tetraonidae, with special reference to males. Viltrevy 7:183-596.

Hjorth, I. 1976. The divalent origin and adaptive radiation of grouse songs. Ornis Scand. 7:147-157.

Ivanter, E. V. 1962. K biologii ryabchika v Karelii. Ornitologiya 4:87-98. (In Russian)

Jenkins, D., A. Watson & G. R. Miller. 1963. Population studies on red grouse, Lagopus lagopus scoticus (Lath.) in north-east Scotland. J. Anim. Ecol. 32:317-376.

Jönsson, I. K., P. K. Angelstam & J. E. Swenson. 1991. Patterns of life-history and habitat in Palaearctic and Nearctic forest grouse. Ornis Scand. 22:in press.

Klaus, S., J. Wiesner & R. Bräsecke. 1975. Revierstruktur und Revierverhalten beim Haselhuhn (Tetrastes bonasia L.). Beitr. Jagd- und Wildforsch. 9:443-452.

Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. J. Anim. Ecol. 47:461-475.

Marzluff, J. M. & R. P. Balda. 1988. Resource and climatic variability: influences on sociality of two southwestern corvids. Pp. 255-283 in C. N. Slobodchikoff, ed. The ecology of social behavior. Adademic Press, New York.

Moss, R. & I. Hanssen. 1980. Grouse nutrition. Commonwealth Bur. Nutr., Nutr. Abstr. Rev.--Ser. B. 50:555-567.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge.

Pulliam, H. R. & G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biol. 6:169-197.

Pynnönen, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, Tetrastes bonasia (L.). Pap. Game Res. 12:1-90.

Rolstad, J. & P. Wegge. 1987. Habitat characteristics of capercaillie Tetrao urogallus display grounds in southeastern Norway. Holarct. Ecol. 10:219-229.

Sæther, B.-E. & R. Andersen. 1988. Ecological consequences of body size in grouse Tetraonidae. Fauna norv. Ser. C, Cinclus 11:19-26.

Scherzinger, W. 1979. Zum Fiendverhalten des Haselhuhnes (Bonasa bonasia). Vogelwelt 100:205-217.

Scherzinger, W. 1981. Stimminventar und Fortpflanzungsverhalten des Haselhuhnes Bonasa bonasia. Ornithol. Beob. 78:57-86.

Seiskari, P. 1962. On the winter ecology of the capercaillie, Tetrao urogallus, and the black grouse, Lyrurus tetrix, in Finland. Pap. Game Res. 22:1-119.

Stamps, J. A. & K. Tollestrup. 1984. Prospective resource defense in a territorial species. Am. Nat. 123:99-114.

Sugimoto, M. 1986. Captive breeding and behavioral analysis of the hazel grouse Tetrastes bonasia. Thesis, Obihiro Univ. of Agr. and Vet. Med., Obihiro, Japan.

Watson, A. & D. Jenkins. 1964. Notes on the behaviour of the red grouse. British Birds 57:137-170.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev.

Ecol. Syst. 7:81-120.

Winkler, H. & B. Leisler. 1985. Morphological aspects of habitat selection in birds. Pp. 415-434 in M. L. Cody, ed. Habitat selection in birds. Academic Press, Orlando, Florida.